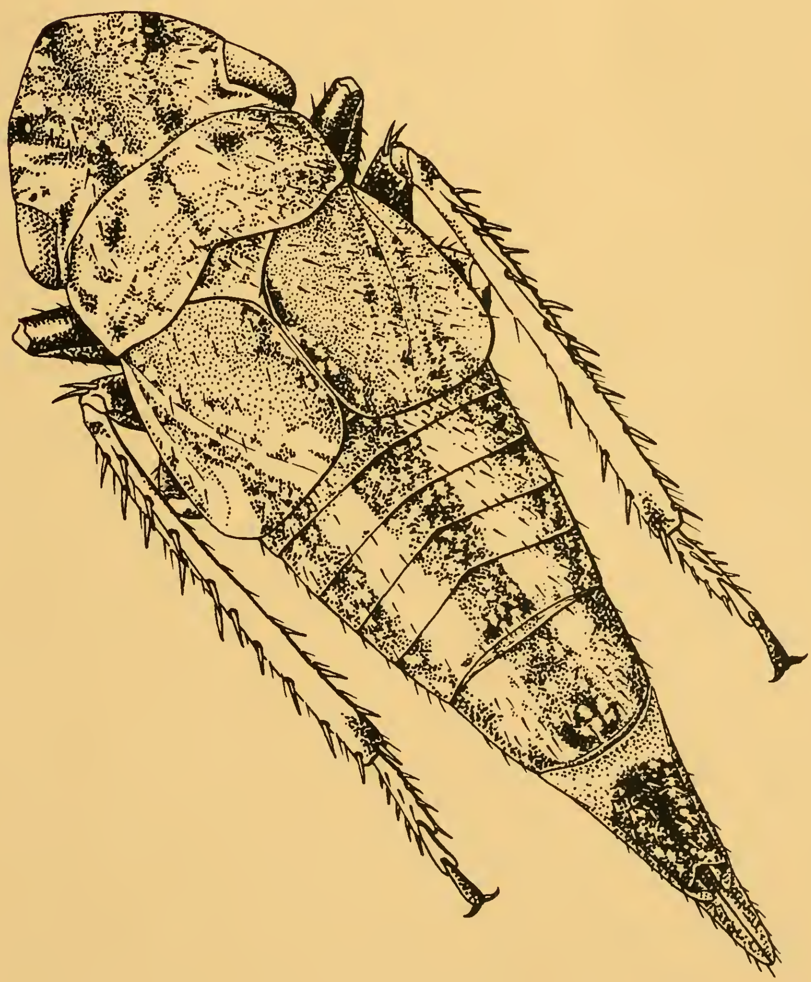
# GREAT BASIN NATURALIST MEMOIRS

Number 12 Brigham Young University 1988



# Research in the Auchenorrhyncha, Homoptera: A Tribute to Paul W. Oman



GREAT BASIN NATURALIST



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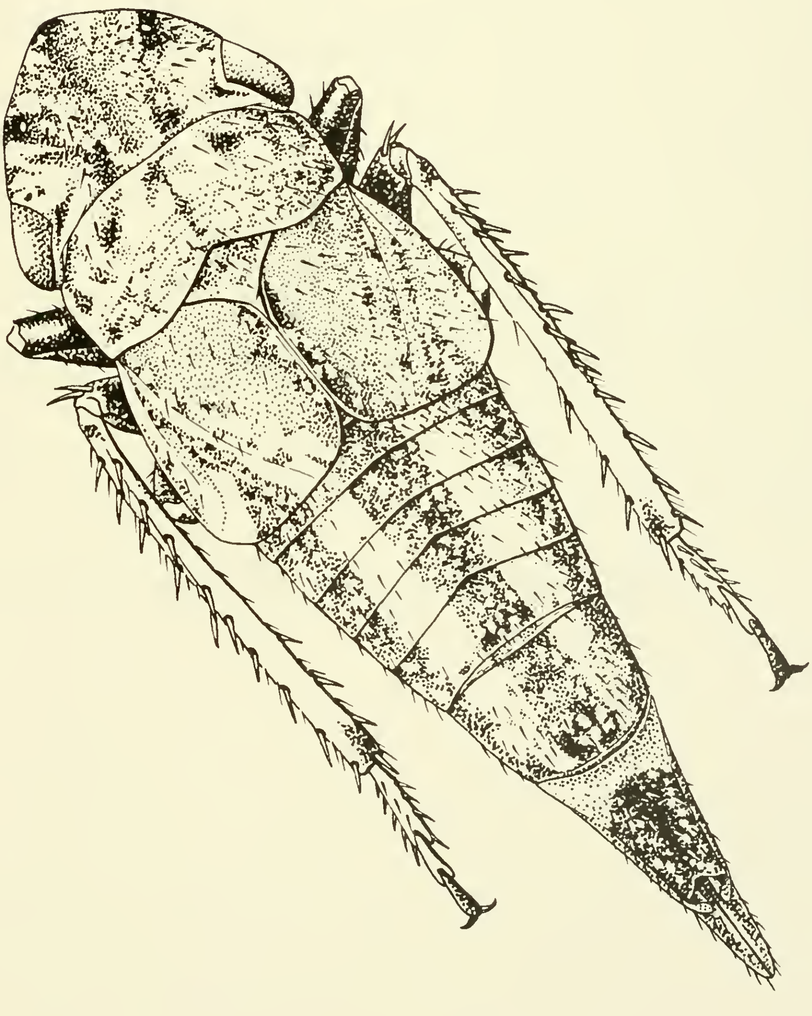
# Research in the Auchenorrhyncha, Homoptera: A Tribute to Paul W. Oman



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Great Basin Naturalist Memoirs

# Research in the Auchenorrhyncha, Homoptera: A Tribute to Paul W. Oman

No. 12 Brigham Young University, Provo, Utah 1988

## PREFACE

A committee was formed late in 1986 to organize and develop a volume of taxonomic papers on the Auchenorrhyncha, Homoptera to honor Dr. Paul W. Oman for his outstanding contributions in leafhopper systematics. This volume is the result of efforts by the committee and by contributors to the work. The 15 papers form not only a dedicatory treatise of Auchenorrhyncha systematics, but also a printed emblem of esteemed appreciation to Dr. Oman for his untiring efforts and many years of dedicated service in promoting leafhopper systematics in particular and the entomological sciences in general.

The biography of Dr. Oman, prepared by his long-time associate John Lattin, and a special review of the biology, morphology, and evolution of leafhoppers by the Australian taxonomist, John Evans, comprise part of the volume. The remainder consists of a selected group of 10 taxonomic papers on leafhoppers, three on planthoppers, and one on cicadas. The scope of these papers ranges from the description of a single taxon to a full taxonomic treatment of a higher category (subfamily). Each paper offers important data on the biogeography of the respective group. Others cover host plant associations and relationships, phylogeny, and numerical taxonomy.

Authors of the volume are long-time friends and associates of Dr. Oman, including a former graduate student, Dr. C. A. Viraktamath. A symposium organized by H. Derrick Blocker and Paul H. Freytag was held at the 1988 Annual Meeting of the Entomological Society of Louisville, Kentucky. The culmination of this symposium was the keynote address by Robert F. Whitcomb, the presentation of papers, and the presentation of a bound copy of this volume to the honoree by Mervin W. Nielson.

The committee expresses appreciation to Dr. Stephen L. Wood, editor of *The Great Basin Naturalist*, Brigham Young University, for his efforts in editing and preparing the volume for publication. We also acknowledge

Mrs. Terry Simmons and Mrs. Karen Jensen, Monte L. Bean Museum, Brigham Young University, for their invaluable assistance in typing those manuscripts that required conversion to the IBM WordPerfect system.

Mervin W. Nielson,
Coordinator

H. Derrick Blocker
Paul H. Freytag
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James P. Kramer
Robert F. Ruppel

ORGANIZING COMMITTEE

# PAUL W. OMAN—AN APPRECIATION

John D. Lattin[1]

ABSTRACT.—The contributions to professional entomology made by Paul W. Oman are reviewed. A bibliography of his published contributions to this field from 1930 to 1987 is included.

I first met Paul Oman in December 1950 in Denver, Colorado, at the national meeting of the Entomological Society of America. He was in the uniform of the U.S. Army with the rank of major, having been called up again to serve in the Korean War (or "ruckus" as Paul preferred to call it). I was a graduate student at the University of Kansas, working with H. B. Hungerford. Dr. Hungerford encouraged me to attend the meeting, as did the other faculty members. He took special care to introduce the graduate students to other entomologists at the meeting, including Paul Oman, himself a graduate of the University of Kansas. My recollection of that meeting was that Paul took special interest in each student he met, even though his time was limited and he was quite busy with society affairs. He still takes time to meet and work with students. Now, thirty-eight years later, we share the same department, coffee room, Systematic Entomology Laboratory (OSU), and a good many hours of collaboration and discussion in and out of the field.

Paul Wilson Oman was born in Garnett, Anderson County, Kansas, on 22 February 1908. He grew up on a farm about five miles outside of Garnett. His early education was in a rural school close to his home. He had to commute the five miles when he later entered Garnett High School. While growing up, he made the usual collections of natural history objects, including insects. A high school biology teacher was particularly influential in keeping alive Paul's interest in the natural sciences.

He first attended the University of Kansas at Lawrence to strengthen his background in mathematics and English, since he was considering the possibility of a career in the Navy, including attending Annapolis. He took a course in entomology to satisfy a biological science requirement and soon transferred to that department. Among the departmental faculty were H. B. Hungerford, chairman, K. C. Doering, P. B. Lawson, R. H. Beamer, and P. A. Readio. It is interesting to note that Hungerford (my own major professor in 1950) worked on aquatic Hemiptera, Readio on the Reduviidae, Kathleen Doering was a morphologist but worked on Homoptera, and both Lawson and Beamer worked not only on Homoptera but also on leafhoppers. Not surprisingly, Paul's interest in this group of insects was kindled at K.U., and he has continued to work on the family during his entire scientific career.

Paul Oman made a fine academic record at the University of Kansas, being elected to Sigma Xi, Phi Sigma, and Phi Beta Kappa in 1930. Prior to that date he had been elected to the Pen and Scroll in 1927—an honorary society in the English Department. Those who have read Paul's papers or corresponded with him know that this award was well deserved and know too that he likes to communicate via the written memo. He graduated from the University of Kansas with an A.B. in entomology in the spring of 1930.

Paul joined the recently organized Taxonomic Unit of the Bureau of Entomology, U.S. Department of Agriculture, in October 1930. This was to be a long association, for he retired from the USDA in 1967 when he joined the faculty of the Department of Entomology at Oregon State University. His responsibilities included the auchenorrhyncous Homoptera and the Psyllidae. Thus, his interests in the Homoptera, fostered by the faculty at the University of Kansas, provided

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Fig. 1. Paul W. Oman.

his entrée into his profession. The need for a specialist in the "hard" Homoptera was prompted by the extensive ecological work being done on the beet leafhopper and associated insects, especially in the Twin Falls, Idaho, region. This fortuitous association with *Circulifer tenellus* (Baker), a vector of "curly-top" of beets in the western United States, also provided a basis of his lifelong interest in applied systematics—the application of systematic techniques toward the solution of problems of concern to society. His ultimate discovery that this insect was native to the Middle East (rather than South America as some thought) (Oman 1936, 1948) lead to explorations for biological control agents from the Middle East. Further, this discovery strengthened his conviction that systematics should play an important role in biological control. Some years later, when he assumed charge of the entomological taxonomic unit of the USDA, he was instrumental in adding the biological control unit, resulting in the joint organization we see today.

During his early years in Washington, D.C., he attended evening classes at George Washington University where he majored in entomology. He had extra courses from the University of Kansas, and these, together with his course work transferred to Lawrence from George Washington, plus a thesis, resulted in an M.A. degree in entomology from the University of Kansas in 1935. Not surprisingly, his thesis was on the leafhoppers and entitled "A Generic Revision of American Bythoscopinae and South American Jassinae," later published in the well-known University of Kansas Science Bulletin (Oman 1938). He continued his academic work at George Washington University as time permitted and received a Ph.D. degree from that institution in 1941. His thesis, somewhat revised, appeared under the title, "The Nearctic Leafhoppers (Homoptera: Cicadellidae), a Generic Classification and Check List" (Oman 1949). As Z. P. Metcalf stated (1950, Ann. Entomol. Soc. Amer. 43: 458), "This is one of the most outstanding recent contributions to the study of one of the most difficult families of the Homoptera," and indeed it was. Paul produced this landmark publication by working quietly, steadily, and efficiently, and accomplishing a great deal—a Paul Oman hallmark. He was working as a taxonomic specialist at this time, and so the courses and thesis work were done largely after hours. He was the scientist responsible for research on the Auchenorrhyncha. The hiatus between the completion of his dissertation and the appearance of the published version was caused by World War II.

Paul Oman entered the U.S. Army as a first lieutenant in the Medical Corps in October 1942 and was assigned to the South Pacific and the Far East commands. He served in that area, being promoted to captain, until he returned and left active service in February 1946. While in the South Pacific, he was responsible for the organization and direction of entomological activities on Guadalcanal (November 1943–February 1945) and Okinawa (April–June 1945). Although other medical entomology problems were involved, the control of malaria vectors was the chief effort in both locales. The details of some of these activities can be found in Oman and Christenson (1947) and Harper, Downs, Oman, and

Levine (1963). At the time of his discharge from the U.S. Army and his return to the Division of Insect Identification, USDA, he could hardly anticipate that the experience gained in medical entomology would be used again—in 1950, when he was recalled into the Army to serve three years in the Korean War.

During the four years following his return from the South Pacific, Paul was deeply involved in the auchenorrhynchous Homoptera. He became project leader in the Hemiptera and ultimately assistant division leader of the Division of Insect Identification. He published a number of papers, including his 253-page generic classification of the Nearctic leafhoppers, as well as an account of some of the medical entomology work done in the South Pacific. His interest in applied systematics is reflected in the papers of this period.

In September 1950 he was reactivated to regular duty in the U.S. Army at the rank of major and assigned to the Far East during the Korean War. His first assignment was as entomologist, Headquarters, 3rd Army. Later he became chief of the Department of Entomology, 406th Medical General Laboratory in Tokyo, and then commanding officer, Far East Medical Research Unit, the position he held until his discharge in August 1953. He published several papers dealing with medical entomology during this time, and, of special note to homopterists, a paper describing three new species of *Errhomus* with a key to the species. I doubt that he ever thought he would devote many of his later years to an intensive study of the genus *Errhomus* (Oman 1987), but we are glad he did.

Once again he was discharged from the U.S. Army and again returned to the U.S. Department of Agriculture, this time as the head of what became the Insect Identification and Parasite Introduction Research Branch, Agricultural Research Service. His systematic work continued, as did his deep involvement in all aspects of entomology, entomological administration, and the Entomological Society of America. Gradually, his writing began to reflect his increased responsibilities and his ever-broadening interests, but always there was a deep interest in the leafhoppers.

Part of his administrative responsibilities involved increased international activities. He was the leader of the United States entomological delegation to the USSR in 1959 under the U.S.-USSR Scientific and Cultural Exchange Program. In October 1960 he moved to New Delhi, India, to become the director, Far East Regional Research Office, Foreign Research and Technical Programs Division, ARS, USDA. There he was responsible for all technical and administrative aspects of agricultural research studies in Asiatic countries where Public Law 480 funds were available for research of mutual interest to the United States and the foreign country.

Paul returned home from India in December 1962 to become assistant to the director, Entomology Research Division, ARS, USDA. A year later he was appointed assistant director of the Entomology Research Division, a position he retained until he retired from the U.S. Department of Agriculture in 1967. Paul's responsibilities included all extramural research programs, chairman of the Division Committee for the evaluations of research personnel, administration of divisional laboratories, and an active role in the planning and development of programs and policies of the Entomology Research Division. Still he continued to publish, chiefly on topics related to his responsibilities with the Division, but he found time to initiate and participate in the first conference under the new U.S.–Japan Cooperative Science Program. This conference, held in Japan, dealt with arthropod-borne plant viruses (Maramorosch and Oman 1966). He was responsible for another U.S.-Japan Conference held in Washington, D.C., in 1967. This time the subject matter was "Systematics in Relation to the Geographical Distribution of Insects in the Pacific." Paul Oman and Karl V. Krombein were the organizers for the United States. It was obvious that Paul was held in high regard by his Japanese colleagues. I was pleased to have been a participant in that gathering; it was a special occasion. By this time Paul had retired after 37 years with the U.S. Department of Agriculture and had joined the faculty of the Department of Entomology at Oregon State University, and yet another chapter had begun in his productive career. He still maintains active connections with the USDA, and, even as this is being written, he is assisting them to resolve a problem dealing with the Homoptera.

Paul W. Oman, now Professor Paul W. Oman, joined the departmental faculty in the

fall of 1967. He assumed many of my responsibilities in systematic entomology when I moved into administration. Characteristically, he launched into his new career with great energy. He developed his own course in systematic entomology, developed a course in advances in pest management, and began to direct graduate student studies. His enormous experience in all aspects of entomology made him a highly valued member of the department, and his advice was sought (and still is) on many topics. As program director at Oregon State University, he participated in the NSF-funded Inter-University Program in Pest Population Ecology that ran from July 1969 until August 1975, a forerunner of the IPM programs at OSU we know today. Most of the leading ecologists of the world were brought to our campus (and other campuses as well) under this program. It was obvious that pest problems were universal problems, and solid science was required to solve them. During this time educational turmoil was everywhere, but these well-organized programs provided some academic stability during unstable times. The Pest Population Ecology program provided a solid core upon which was built a revised curriculum.

It took him less than a year to obtain funding from the National Science Foundation for his work on the systematics of the leafhoppers. This funding extended from 1968 until he retired in 1975. Again, his publications reflected his efforts and interests as he published a series of leafhopper papers. At the same time, he was publishing papers dealing with other aspects of his activities. He also renewed his interest in the genus *Errhomus* and spent many seasons in the field carefully documenting the complex systematic and biogeographical problems associated with that taxon. The result, of course, is the superb monograph on *Errhomus* that appeared in 1987. While many people would be content to stop there, even before the publication was in press he took up the world catalog project with Bill Knight and Merv Nielson. Complacency is not a characteristic of Paul Oman.

Paul was curator of the Entomology Museum from 1967 to 1971. It must have seemed like child's play after having been responsible for the entire systematic operation of the USDA, and yet he took it very seriously and made major strides in establishing sound protocol for the management of the collection. He added many needed books and sought out reprints from major systematists. An active effort was made to acquire, mount, label, and accession thousands of specimens. He made a special effort to develop the Homoptera collection that had languished. During the years since his release as official curator, he has added literally tens of thousands of specimens to the collection, and still continues to add more. These specimens are all mounted, labeled, and, if leafhoppers, identified, and curated. Talk about a curator's dream! We all know that collections become major scientific resources because of the work of many people with a common goal. Paul is the epitome of such a person.

During the ensuing years he served entomology in many ways. He was on the editorial board of the Annual Review of Entomology from 1972 to 1976. He was chairman of the ad hoc Committee on Entomological Collections in the United States. He was a member of the Entomological Society of America Advisory Committee on Systematic Resources in Entomology from 1973 to 1975. He was a member of the National Policy Advisory Committee (NSF) for the National Drosophila Species Resource Center in 1975. He was secretary of a study team that prepared a 138-page report in 1978 entitled "Biological Agents for Pest Control: Status and Prospects" for the USDA in cooperation with land-grant universities, the State Department of Agriculture, and the Agricultural Research Institute.

When his long-time friend and colleague, Knud Swenson, then chairman of our department, was forced to step down because of a tragic illness, Paul took over as acting chairman. He served in that capacity from 1973 to 1974 while the department sought a new department chair. His long experience in science administration was most evident during that time, and we were able to experience yet another facet of his skills. He was a low-key, but a most efficient and effective, administrator. He paid attention to detail and provided leadership and stability that created an atmosphere of professionalism. He rarely complained and favored working out a solution to a problem. Because his dedication to the job at hand was always evident, people responded in a similar fashion. He was especially effective in getting the most out of the resources available to him.

Paul Oman retired in 1975—again. There was only an imperceptible change before and after this date—occasionally he would head for the golf course if the afternoon was especially nice. Although I have never played golf with Paul, I know some who have—be prepared for a fierce competitor and don't wager very much on each hole. During the past 13 years of his "retirement" he has averaged six to eight hours a day in his office, has spent hundreds of hours in the field throughout the West, has given many reading and conference courses to many students, has served on numerous graduate student committees, has hosted foreign scientists and freely shared with them his vast experience with the Cicadellidae, and has identified thousands of leafhoppers for many individuals and institutions.

One of my most recent interactions with Paul occurred on 16 March 1988, when he participated in the program planning session for Adam Asquith, one of my new doctoral students. Paul had given Adam a reading and conference course in zoological nomenclature during the preceding three months. In fact, one of the other graduate committee members brought a particularly knotty problem on nomenclature to the meeting. Ultimately, the problem was resolved by Paul and Adam. Paul brought several current articles from science that were appropriate to the graduate program and the proposed thesis topic. He has always given help freely to the students and faculty, and he did so again on 16 March 1988. His eightieth birthday had been celebrated three weeks earlier, and he had supposedly retired in 1975, but for Paul Oman it was just a regular day.

As one who has known him since 1950, I can attest to his many contributions and deep devotion to entomology. He joined the ESA in 1929, served as president in 1959, was elected an honorary member in 1975, and received the Woodworth Award from the Pacific Branch in 1982. He joined our faculty in 1967, and while he holds the title Emeritus Professor of Entomology, his efforts are indistinguishable from those of regular faculty members. He is one of those rare scientists whose influence has extended far beyond his office and laboratory. I cherish our friendship.

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# SOME NEW CICADELLIDS FROM GRASSLANDS OF KARACHI, PAKISTAN (HOMOPTERA: CICADELLIDAE)

Manzoor Ahmed[1], A. Qadeer[1], and K. F. Malik[1]

ABSTRACT.—A brief survey of grassland leafhoppers of Karachi during 1985 revealed the existence of five new species of the family Cicadellidae. These include *Exitianus major*, *E. minor*, *Chiasmus karachiensis*, *C. lobosa*, and *Goniagnathus bifurcatus*.

Recent studies of grassland leafhoppers of Pakistan by Ahmed (1986), Ahmed and Rao (1986), and Ahmed and Yunus (1986) showed that leafhoppers form a very important component of the phytophagous fauna of our grasslands. The leafhopper fauna described by these and other workers, e.g., Blocker et al. (1972) from USA and Theron (1982) from South Africa, appears to be widely diversified. Andrezejewska (1984) believed that species composition of Auchenorrhyncha in grasslands depends to a high degree on immigrant species, which indicates that most of the species encountered in grasslands move in from the neighboring crops when the latter are harvested. Thus, grasslands serve not only as alternate feeding grounds for leafhopper pests of a number of crops but also as breeding places for many species of leafhoppers during their off-crop seasons. Studies of grassland leafhoppers could therefore be useful from many aspects.

The leafhoppers described herein have been studied following the methodology outlined by Ahmed (1985).

## *Exitianus* Ball

The genus *Exitianus* Ball is known from all major regions of the world. Oman (1949) redescribed the genus and listed the Nearctic species. Metcalf (1967) listed 35 world species, and Ahmed and Rao (1986) recorded *E. capicola* (Kb.) and described *E. peshawarensis* from Pakistan. During the present study two more new species of the genus were collected from Karachi, Pakistan, and are described below.

## *Exitianus major* Ahmed & Qadeer, n. sp.

(Figs. 1 A-K)

LENGTH.—Male 4.2 mm, female 4.8 mm; head broad, rounded at anterior apex; median length of crown nearly equal to or slightly less than the interocular width; transocular width of head slightly more than midlength of crown; ocelli close to mesal margin of eyes on anterolateral margin; crown with dim brown markings, transverse band of dark brown color in middle, rest of crown pale brown; frontoclypeus narrowing anteriorly; anteclypeus longer than broad, narrowing anteriorly; lora broad; pronotum possessing tiny spots of brown color on disc; scutellum dim brown, with two brownish spots anterolaterally.

Forewings with apex smoothly rounded; maximum width slightly prior to midlength; appendix broad, extending around wing apex up to 4th apical cell; apical cells 5; subapical cells 3; veins in the basal region possessing brownish markings all along; hind wings with 4 closed apical cells.

MALE.—Plate in ventral view broad in basal half, narrowed in apical half, possessing 6–7 macrosetae on ventrolateral surface; pygofer with posterior margin extended into narrow posterodorsal lobe, with one long and one small blackish macrosetae on lobe, style in dorsal view massive, sclerotized in marginal areas, membranous in middle, with broad, bluntly rounded lobe, apical extension spinose, curved laterad; connective Y-shaped with arms quite close to each other; aedeagus with preatrium reduced, dorsal apodeme well

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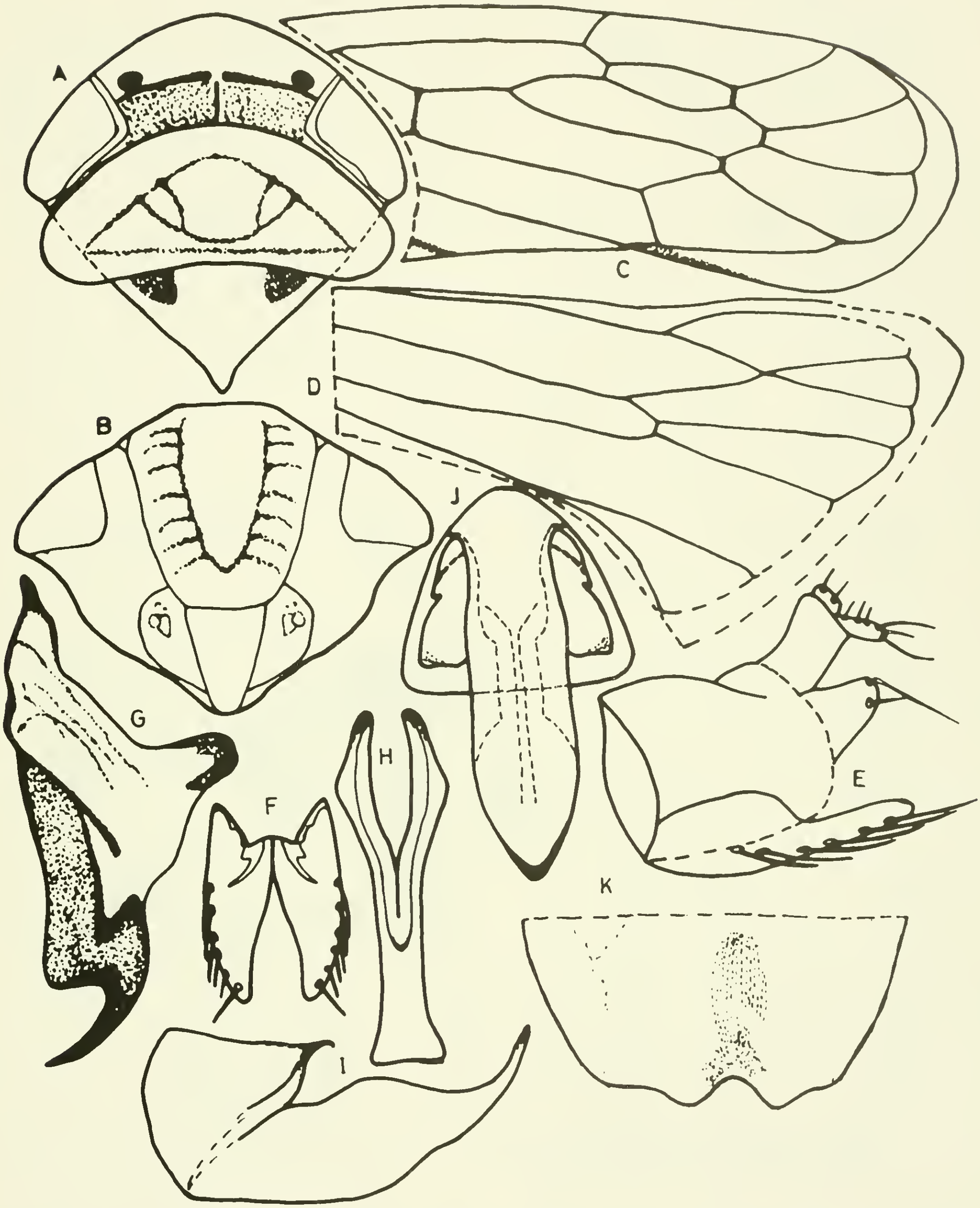



Figs. 1 A-K. *Exitianus major*, n. sp.: A, head and thorax, dorsal view; B, head, ventral view; C, forewing; D, hind wing; E, genital capsule, lateral view; F, male plate, ventral view; G, style, dorsal view; H, connective, dorsal view; I, aedeagus, lateral view; J, aedeagus, dorsal view; K, female seventh sternum.

developed, shaft in lateral view broad in basal 2/3, narrowed apically, smoothly curved dorsally at apex.

FEMALE.—Seventh sternum narrowed posteriorly, posteromedian margin sinuate.

*Exitianus major* appears quite close to *E. capicola* (Stal) in venation and shape of aedeagus, but differs in its smaller size, shape of connective, chaetotaxy of male plate, and to some extent in the shape of female seventh sternum.

HOLOTYPE (male).—PAKISTAN: Karachi, grass,

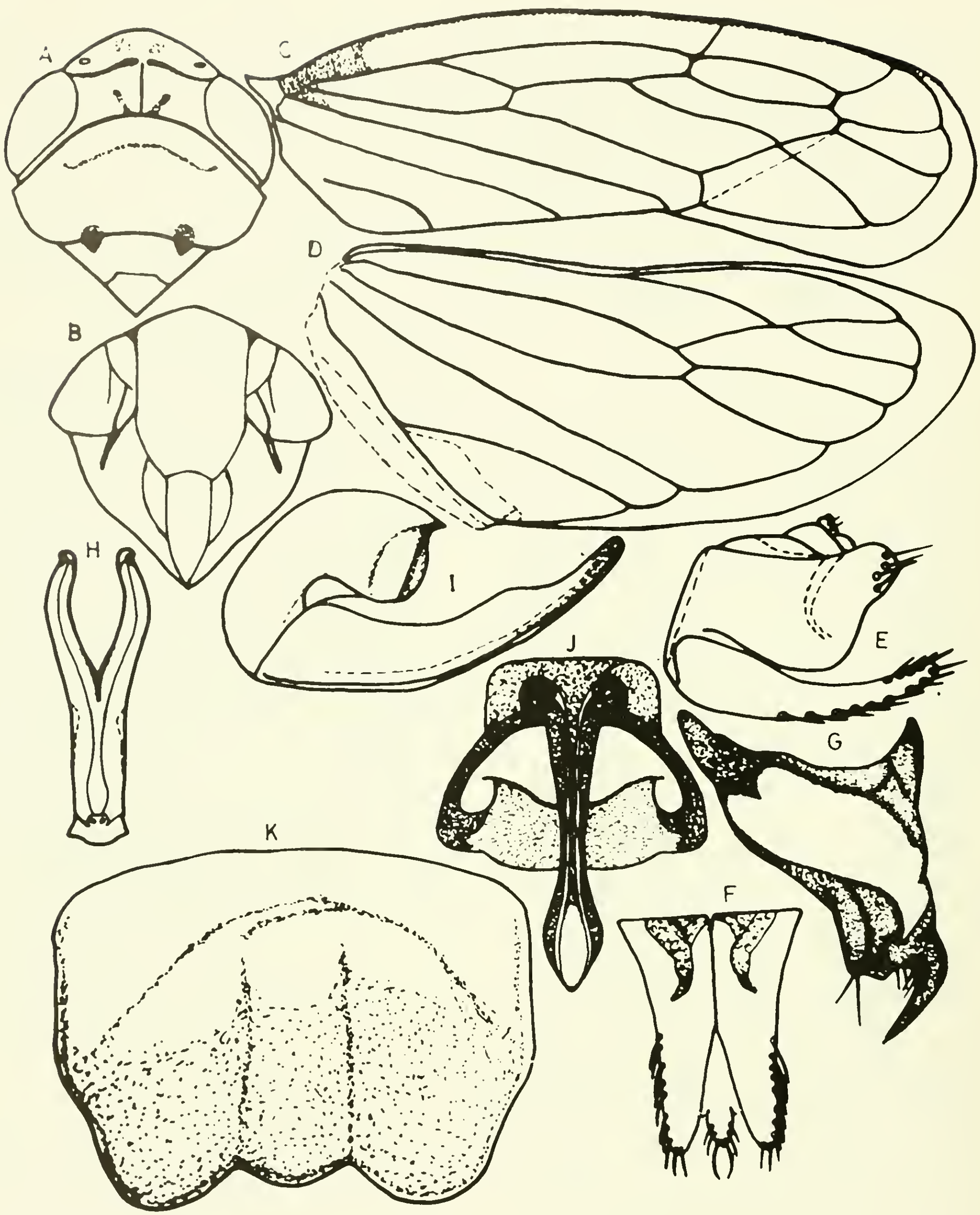



Fig. 2 A-K. *Exitianus minor*, n. sp.: A, head and thorax, dorsal view; B, head, ventral view; C, forewing; D, hind wing; E, genital capsule, lateral view; F, male plates, ventral view; G, style, dorsal view; H, connective, dorsal view; I, aedeagus, lateral view; J, aedeagus, dorsal view; K, female seventh sternum.

26.VI.85, Qadeer. Seven paratypes, same data as holotype, all in Zoological Museum, University of Karachi, Karachi, Pakistan.

*Exitianus minor* Ahmed & Qadeer, n. sp.
(Figs. 2 A-K)

LENGTH.—Male 4.00 mm, female 4.5 mm; head projected in front, broadly rounded at anterior apex; median length of crown less than interocular width; transocular width of head nearly equal to transverse width of pronotum; coronal suture present up to more than midlength; ocelli on anterolateral margin

of crown, close to eyes; crown with brownish markings on disc and transverse brownish band at the level of anterior margin of eyes; ground color of crown more or less pale brown; frontoclypeus nearly parallel sided, narrowed at apex; anteclypeus narrowed anteriorly, much longer than broad; lora broad; pronotum with some tiny spots in middle in anterior region, with posterior margin nearly transverse; scutellum pale brown, with oval-shaped, brownish spots anterolaterally.

Forewing with apex broadly rounded; apical part slightly broader than basal part; appendix broad, extending up to 5th apical cell; apical cells 5; subapical cells 3; hind wing with 4 closed apical cells.

MALE.—Plate in ventral view, broad basally, narrowed apically, possessing 4–5 macrosetae near apex on lateral margin, long row of 9–10 macrosetae from near base to apex on ventral surface; pygofer with posterior margin directed into posterodorsal broad and rounded lobe, lobe possessing 4–5 brownish macrosetae; style in dorsal view massive, membranous in middle, sclerotized along margins, preapical lobe flattened, almost truncate mesally, possessing 3–4 macrosetae, apical extension prominent, spinose, extreme apex directed caudolaterad; connective Y-shaped, with arms smaller than the stem, converging at their apex; aedeagus in lateral view, with preatrium reduced, dorsal apodeme present, appearing broad in dorsal view, shaft tubular, curved smoothly dorsad, apical part narrowed.

FEMALE.—Seventh sternum with posterior margin possessing three lobes, lateral lobes more projected than the median.

*Exitianus minor* appears close to *E. karachiensis* Ahmed and *E. major* described hitherto in its venation and general pattern of male genitalia, but differs in its shape of connective and female seventh sternum.

HOLOTYPE (male).—PAKISTAN: Karachi, grass, 12.V.1985, Qadeer. Thirty paratypes, all in Zoological Museum, University of Karachi, Karachi, Pakistan.

### *Chiasmus* Mulsant and Rey

Distant (1908) recorded *Chiasmus uzelli* Melichar from Ceylon. Pruthi (1930) described three new species from various parts of India and reassigned *Kartwa mustelina* Distant to the genus *Chiasmus*. The present description of two new species in *Chiasmus* is the first record of the genus from Pakistan.

### *Chiasmus karachiensis* Ahmed & Qadeer, n. sp.
(Figs. 3 A-J)

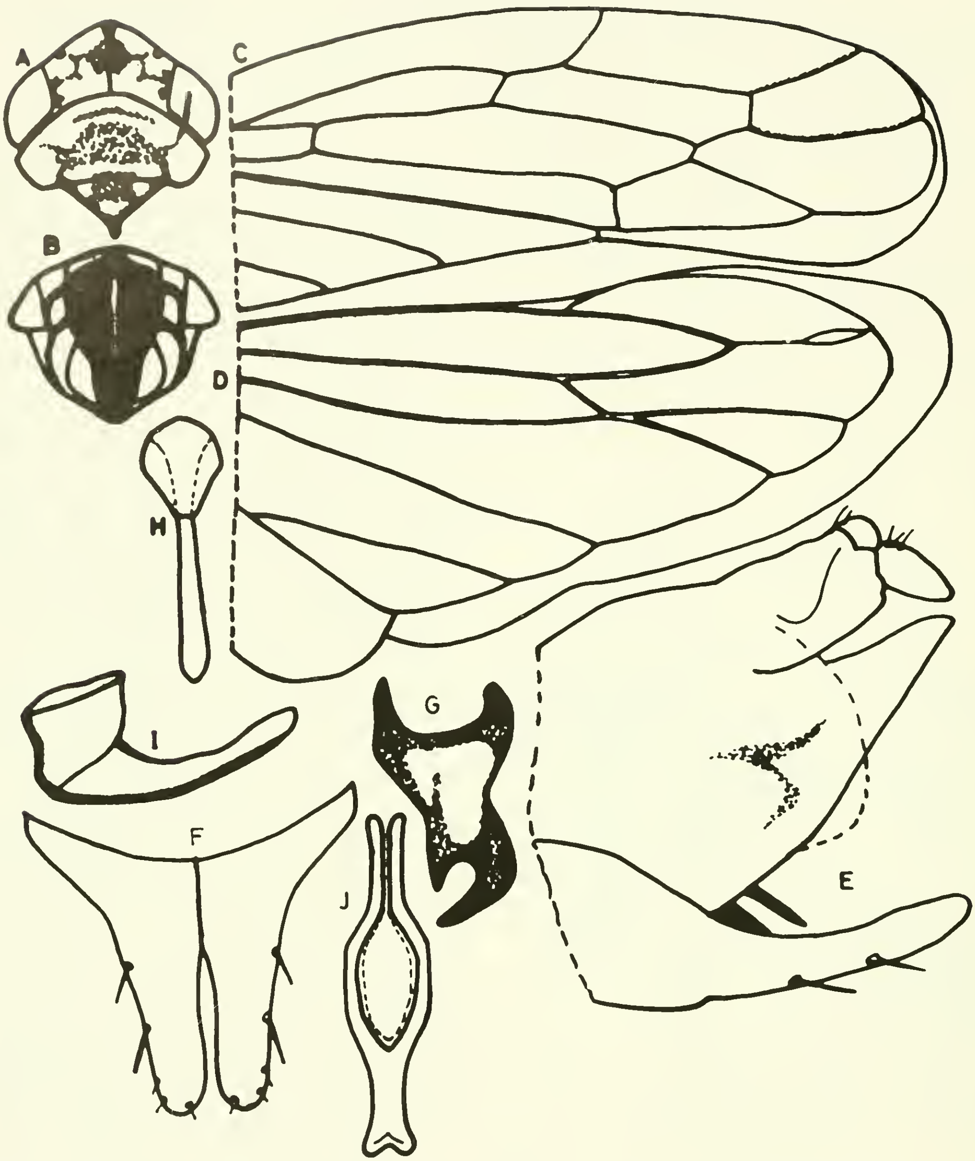
LENGTH.—Male 2.3 mm; head strongly projected in front, apex of crown narrowed and rounded; median length of crown much less than interocular width; transocular width of head slightly more than transverse width of pronotum; coronal suture present up to more than midlength of crown; ocelli on anterolateral margin of crown, close to eyes; color of eyes blackish; crown possessing blackish brown dots throughout; ground color of crown pale yellow; pronotum yellowish, its posterior margin nearly straight; scutellum dim yellow; frontoclypeus narrowing anteriorly, blackish in color throughout, except median, longitudinal stripe of yellow color; anteclypeus black in middle; lora broad, expanded.

Forewing with apex smoothly rounded; maximum width of wing slightly prior to midlength; appendix broad, extending to 3rd apical cell; apical cells 4; subapical cells 2; hind wing with 4 closed apical cells.

MALE.—Plate in ventral view broad at base, middle and apical parts much narrowed, macrosetae 2–3 on ventral surface in apical half, apex of plate rounded and directed caudad; pygofer in lateral view with posterior margin narrowed into angular, posterodorsal, much-projected lobe, processes and setae usually absent; style in dorsal view membranous in middle, sclerotized along margins, preapical lobe short, narrow, and angular, apical extension dark brown in color, spinose and curved laterad; connective Y-shaped, with arms longer than the stem, arms apposed most of their anterior part, forming nearly rounded space in middle; aedeagus in lateral view with preatrium reduced, dorsal apodeme absent, shaft tubular, somewhat curved dorsad towards apex, processes absent.

*C. karachiensis* appears close to *C. alata* Pruthi in general appearance as well as pattern of venation and genitalia, but differs in the shape of pygofer.

HOLOTYPE (male).—PAKISTAN: Karachi, grass, 1.XI.85, Qadeer. One paratype, same data as holotype, both in the Zoological Museum, University of Karachi, Karachi, Pakistan.

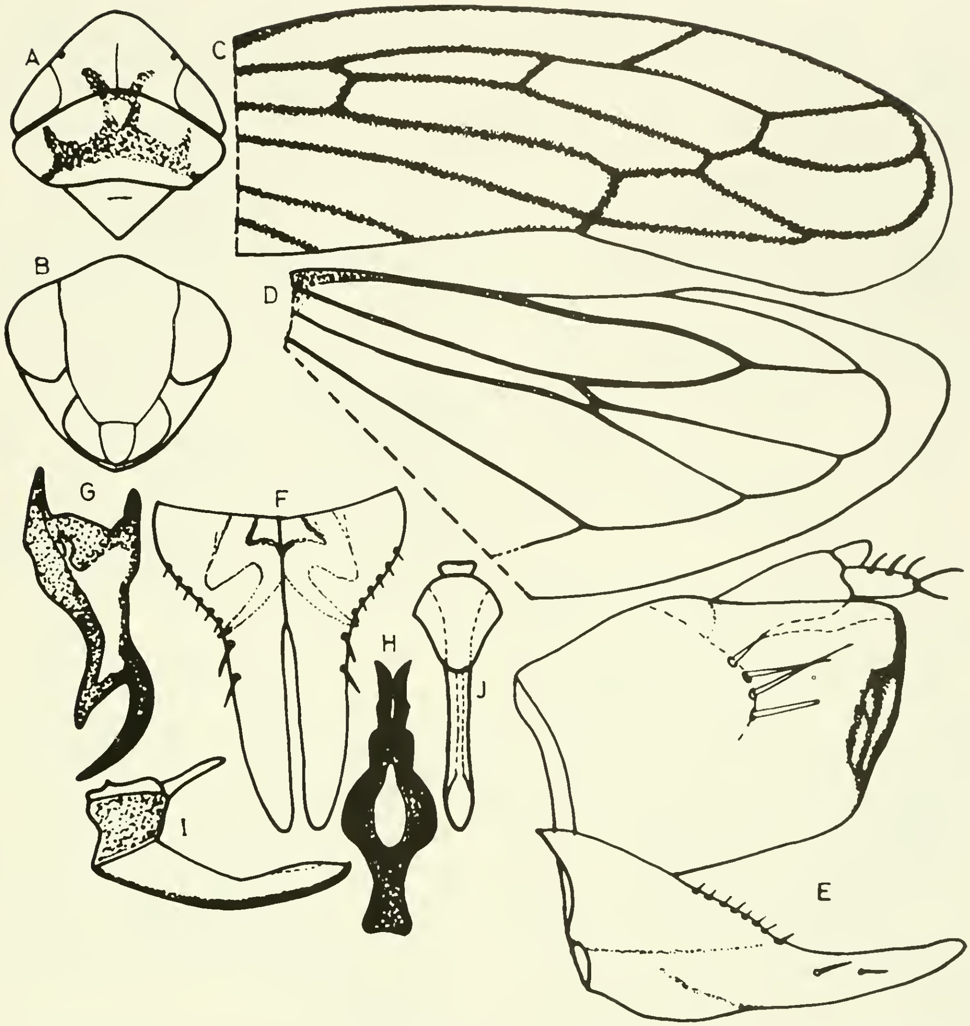



Figs. 3 A-J. *Chiasmus karachiensis*, n. sp.: A, head and thorax, dorsal view; B, head, ventral view; C, forewing; D, hind wing; E, genital capsule, lateral view; F, male plates, ventral view; G, style, dorsal view; H, connective, dorsal view; I, aedeagus, lateral view; J, aedeagus, dorsal view.

*Chiasmus lobata* Ahmed & Qadeer, n. sp.
(Figs. 4 A-J)

LENGTH.—Male 2.5 mm, female 3.0 mm; head projected and narrowed in front, apex rounded; median length of crown nearly equal to or slightly less than interocular width; transocular width of head equal to transverse width of pronotum; coronal suture present up to more than midlength; ocelli present on anterolateral margin of crown, close to eyes; crown possessing few, dim, brownish spots in middle along posterior margin; frontoclypeus broad, narrowed in apical 1/3; anteclypeus longer than broad; lora broad; pronotum possessing rows of brownish markings.

Forewing with apical margin smoothly rounded; apical cells 4; appendix broad, reaching 3rd apical cell; subapical cells 2;




Figs. 4 A-J. *Chiasmus lobata*, n. sp.: A, head and thorax, dorsal view; B, head, ventral view; C, forewing; D, hind wing; E, genital capsule, lateral view; F, male plate, ventral view; G, style, dorsal view; H, connective, dorsal view; I, aedeagus, lateral view; J, aedeagus, dorsal view.

veins with brownish shades along their length; hind wing with 3 closed apical cells.

MALE.—Plate in lateral view broad at base, narrowed in apical half, apex rounded, possessing row of 2–3 macrosetae on ventral surface in apical half, another row of 7–8 microsetae on lateral margin from near base to midlength, length of plate more than the pygofer, apposed mesally at base; pygofer in lateral view with posterior margin broad, dented, more projected posterodorsally, disc with dorsoventral row of 4 macrosetae; anal tube moderately developed; style in dorsal view with preapical lobe narrowed, angular, apical extension thin, spinose, directed laterad; aedeagus in lateral view with preatrium reduced, dorsal apodeme present, shaft tubular, somewhat curved dorsad in middle, apex rounded and thin, directed caudad; connective Y-shaped, with arms much longer than stem, arms confluent again forming space in middle.

*Chiasmus lobata* appears quite close to *C. karachiensis* as well as to *C. niger* Pruthi and *C. jagdishi* Pruthi in the pattern of male genitalia, but differs from them in the peculiar

shape of pygofer, particularly the posterodorsal margin.

HOLOTYPE (male).—PAKISTAN: Karachi, 15.XII.85, grass, Qadeer. One paratype, same data as holotype, both in Zoological Museum, University of Karachi, Karachi, Pakistan.

### *Goniagnathus* Fieber

The genus *Goniagnathus* Fieber was redescribed by Dlabola (1954). Distant (1918) described three species of the genus from India. Ahmed and Yunus (1986) reported *G. guttulinervis* Kirsch. from Pakistan. Another species of the genus is described here from grass.

### *Goniagnathus bifurcatus* Ahmed & Qadeer, n. sp.

(Figs. 5 A-I)

LENGTH.—Male 5.0 mm; head with anterior margin broadly convex, smoothly rounded in front; median length of crown much less than the interocular width; transocular width of head slightly more than the transverse width of pronotum; coronal suture up to more than midlength; ocelli on anterolateral margin of head, close to apex; anteclypeus longer than broad; lora broad; pronotum with few brownish black dots along anterior margin and on posterior margin; scutellum grayish black throughout.

Forewing with apex broad and rounded; maximum width of wing in basal half; appendix broad, extending to 4th apical cell; apical cells 5; subapical cells 3; black markings present in appendix, 2nd, 3rd, and 4th apical cells, in some discal subapical cells and along all the veins; hind wing with 4 closed apical cells.

MALE.—Genital segment strongly sclerotized, dark brown in color; plates in ventral view fused completely to form a single ovid structure, width of plate decreasing smoothly to rounded apex, with few blackish macrosetae and marginal microsetae in apical part; pygofer in lateral view with posterior margin broad, nearly truncate, slightly sinuate posterodorsally, with at least three prominent groups of stout macrosetae, one closely placed group posterodorsally, one mixed group of short and long in middle of posterior margin in middle, and one group in posteroventral region of disc, microsetae dispersed throughout pygofer; anal tube moderately long, possessing fine microsetae; posterior margin of pygofer finely dentate; style in dorsal view with preapical lobe minutely developed, apical part expanded, with extreme apex obliquely truncate; connective in dorsal view rod-shaped, arms indistinct, connective curved in middle; aedeagus in lateral view with preatrium reduced, dorsal apodeme well developed, closely associated with connective; shaft of aedeagus short, tapered apically, long processes arising from atrium, subparallel to shaft, exceeding shaft in length; gonopore subterminal on dorsal surface.

*Goniagnathus bifurcatus* is close to *G. guttulinervis* Kirschbaum in the general pattern of male genitalia, particularly the male plate and aedeagus, but differs in the shape of style, pygofer, and connective.

HOLOTYPE (male).—PAKISTAN: Karachi, grass, 10.XI.85, Qadeer. One paratype, same data as holotype, both in Zoological Museum, University of Karachi, Karachi, Pakistan.

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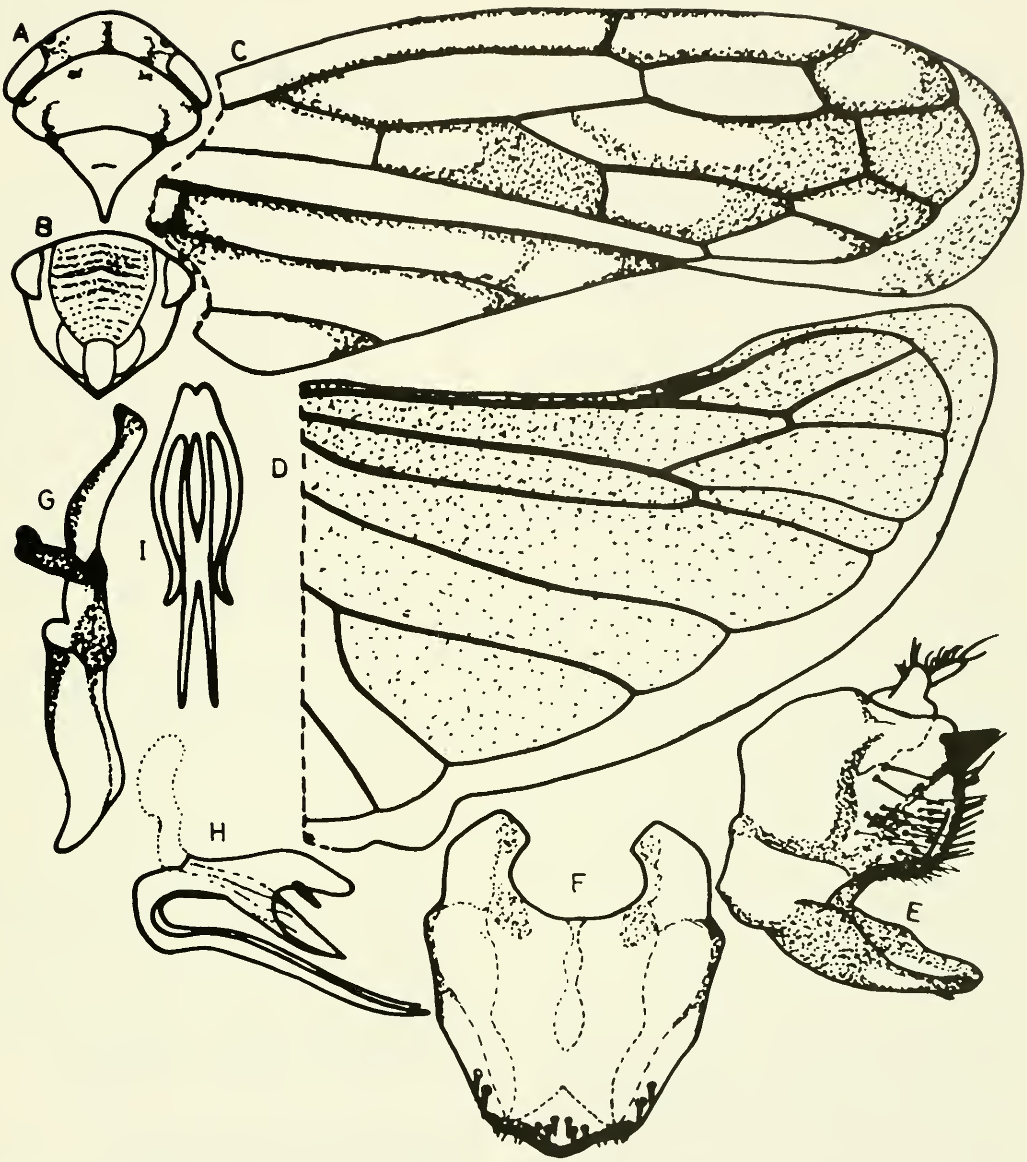


Figs. 5 A-I. *Goniagnathus bifurcatus*, n. sp.: A, head and thorax, dorsal view; B, head, ventral view; C, forewing; D, hind wing; E, genital capsule, lateral view; H, aedeagus and connective, lateral view; I, aedeagus, dorsal view.

# CLASSIFICATION OF THE SUBGENUS *ATHYSANELLA*, GENUS *ATHYSANELLA* BAKER (HOMOPTERA, CICADELLIDAE, DELTOCEPHALINAE)[1]

H. Derrick Blocker[2] and James W. Johnson[3]

ABSTRACT.—The subgenus *Athysanella* Baker is reviewed and a possible phylogeny of the group is discussed. A total of 35 species is recognized. Descriptions, illustrations, and a key to males are presented. Twelve new species are described: *aphoda, cursa, deserta, furnaca, hemijona, krameri, pastora, strobila, stylosa, vativala,* and *whitcombi* are from the western United States, and *marthae* is from Mexico.

The subgenera of *Athysanella* Baker have been reviewed by Blocker and Johnson (1988). The nominate subgenus revised herein contains 35 species, of which 12 are new. Distribution of this subgenus is primarily in the western half of the United States, with 4 species recorded from Mexico and 4 from western Canada. The hosts are primarily shortgrasses.

Blocker (1984) has described the morphological variation that occurs in both sexes because of incompletely developed genital structures. Undeveloped and partially developed specimens are often difficult to identify. We have attempted to illustrate sufficient characters to allow identification of males, but the user must attempt to make identifications from a series of specimens that appear to be fully developed. As an example, the hind tibial spur of partially developed males may be absent or reduced; the genitalia also may be reduced in size.

Females are particularly difficult to determine. It is best to try to associate them with a male and then check the shape of the posterior margin of sternum VII. There is much infraspecific variation in specimens of both sexes. Ball and Beamer (1940) should be consulted for additional and original descriptions; Blocker and Wesley (1985) and Wesley and Blocker (1985) should be consulted for distribution in Canada-Alaska and Mexico, respectively.

## Depositories

Persons and institutions (acronyms are used in the text) furnishing material for this study include (the authors regret any omissions):

UAz – University of Arizona, F. Werner.
CAS – California Academy of Science, P. Arnaud and N. Penny.
CDA – California Department of Agriculture, R. Gill and J. Sorensen.
CNC – Canadian National Collection, K. G. A. Hamilton.
IPL – Insect Pathology Laboratory, USDA, Beltsville, A. L. Hicks and R. F. Whitcomb.
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KU – Snow Entomological Museum, University of Kansas, R. W. Brooks.
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OhSU – Ohio State University, P. S. Cwikla.
OkSU – Oklahoma State University, R. A. Drew.
OrSU – Oregon State University, P. W. Oman.
UBC – University of British Columbia, G. Scudder and S. Cannings.
USNM – U.S. National Museum, Natural History, J. P. Kramer.

## *Athysanella (Athysanella)* Baker

*Athysanella* Baker, 1898: 185. Type species: *Athysanella magdalena* Baker, 1898, by original designation.

This subgenus is characterized by the presence of a hind tibial spur and the absence of a pygofer process (Blocker and Johnson 1988). It is a sister of the subgenus *Gladionura*.

Species of the subgenus *Athysanella:*

*aphoda* Blocker, n. sp. Nevada.
*aspera* Ball and Beamer, 1940. California.
*bifida* Ball and Beamer, 1940. Colorado, Montana, New Mexico, North Dakota, South Dakota, Texas, Wyoming, Canada.
*cursa* Blocker, n. sp. Arizona, Colorado, New Mexico, Utah.
*deserta* Blocker, n. sp. California.
*foeda* Ball and Beamer, 1940. Wyoming.
*fredonia* Ball and Beamer, 1940. Arizona, Colorado, New Mexico, Nevada, Utah.
*furnaca* Blocker, n. sp. California.
*gardenia* Osborn, 1930. Colorado, Wyoming.

[1]Contribution 88-312-J from the Kansas Agriculture Experiment Station.
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*frigida* Osborn, 1930.
*globosa* Ball and Beamer, 1940. Arizona.
*hemijona* Blocker, n. sp. California.
*incerta* Ball and Beamer, 1940. Colorado, Kansas, Montana, Nebraska, New Mexico, Wyoming.
*incongrua* Baker, 1898. Colorado, Iowa, Kansas, Nebraska, New Hampshire, New Mexico, Oklahoma, South Dakota, Texas, Wyoming.
*kadokana* Knull, 1951. Colorado, Montana, Nebraska, South Dakota, Wyoming, Canada.
*kanabana* Ball and Beamer, 1940. Arizona, Kansas, New Mexico, Utah.
*krameri* Blocker, n. sp. California.
*laeta* Ball and Beamer, 1940. Arizona, New Mexico.
*magdalena* Baker, 1898. Arizona, California, Colorado, Montana, New Mexico, Nevada, Oklahoma, Texas, Wyoming, Mexico.
*marthae* Blocker, n. sp. Mexico.
*parca* Ball and Beamer, 1940. Colorado, New Mexico.
*pastora* Blocker, n. sp. New Mexico.
*plana* Ball and Beamer, 1940. California.
*planata* Ball and Beamer, 1940. California.
*robusta* Baker, 1898. Colorado, Montana, Nebraska, North Dakota, Wyoming, Canada.
*montana* Osborn, 1930.
*rostrata* Ball and Beamer, 1940. California.
*salsa* Ball and Beamer, 1940. Kansas, Texas, Mexico.
*strobila* Blocker, n. sp. California, Idaho, Nevada, Oregon.
*stylosa* Blocker, n. sp. New Mexico.
*supina* Ball and Beamer, 1940. Texas.
*tenera* Ball and Beamer, 1940. Nevada.
*terebrans* (Gillette and Baker), 1895. Colorado, Montana, North Dakota, Nebraska, Utah, Wyoming, Canada.
*utahna* Osborn, 1930. Arizona, California, Colorado, Idaho, Nevada, Utah, Oregon, Washington, Canada, Mexico.
*vativala* Blocker, n. sp. Nebraska, North Dakota.
*whitcombi* Blocker, n. sp. Nevada.
*yumana* Osborn, 1930. Arizona, California.

Key to *Athysanella* Males, sensu stricto

1. Style rounded apically; pygofer variable; plates embrowned apically . . . . . . . . . . . . . . . . 2
— Style widened, usually bifid apically; pygofer usually broadly rounded apically; plates variable . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
2(1). Pygofer extended apically; connective, plates, and vertex variable . . . . . . . . . . . . . . . . . . . . . . 3
— Pygofer truncate apically; connective shorter than style; plates truncate apically; vertex usually with fuscous spots . . . . *gardenia* Osborn
3(2). Aedeagus with basal process, unique; plates truncate apically; connective as long as style; vertex without fuscous spots . . . . *robusta* Baker
— Aedeagus simple or with ventral serrations; connective shorter than style; vertex usually with fuscous spots . . . . . . . . . . . . . . . . . . . . . . 4
4(3). Aedeagus with shaft simple, elongate; plates rounded apically, embrowned . . *pastora*, n. sp.
— Aedeagus with shaft shortened, expanded and serrate ventrally; plates truncate apically . . . . . . . . . . . . . . . . . . . . . . . . . *globosa* Ball & Beamer
5(1). Aedeagus with conspicuous apical hook; style exceeding apex of plate; vertex with or without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . 6
— Aedeagus with poorly developed or no apical hook (apical serrated flanges may be present); style variable; vertex with or without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22
6(5). Aedeagus with single apical hook . . . . . . . . . . . 7
— Aedeagus with semicircular apical hook . . . . 20
7(6). Aedeagus not widest basally (may have crests at midlength), not tapered apically; plates rounded apically; vertex with or without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
— Aedeagus widest in basal 1/2, shaft tapered in apical 1/2, apical hook conspicuous; plates usually truncate apically; vertex with or without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . 8
8(7). Aedeagus with distinct lateral tubercles at base of shaft; style with ventral apical arm widened, dorsal arm slender; vertex without fuscous spots . . . . . . . . . *planata* Ball & Beamer
— Aedeagus without distinct tubercles; style with ventral and dorsal arms variable; vertex with or without spots . . . . . . . . . . . . . . . . . . . . . 9
9(8). Style without apical lateral flange, dorsal arm short, wide; plates rounded apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *krameri*, n. sp.
— Style with distinct apical lateral flange or ventral arm expanded laterally, dorsal arm variable, elongate; plates truncate apically . . . . . 10
10(9). Aedeagus with apex of dorsal apodeme expanded; style with dorsal arm elongate . . . . . 11
— Aedeagus with dorsal apodeme rounded; style variable . . . . . . . . . . . . . . . . . . . . . . . . . 12
11(10). Style with dorsal arm slender; vertex with no fuscous spots; smaller in overall size . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *whitcombi*, n. sp.
— Style with dorsal arm more robust; vertex usually with fuscous spots; larger in size . . . . . . . . . . . . . . . . . . . . . . . . . . . . *plana* Ball & Beamer
12(10). Aedeagus with shaft robust, short; style with dorsal apical arm longer, variable apically . . 13
— Aedeagus with shaft less robust; style with dorsal arm rounded apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *aspera* Ball & Beamer
13(12). Style with dorsal arm bulbous apically; aedeagus with apical hook conspicuous, with slight processes at base . . . . . . . . . . . . *aphoda*, n. sp.
— Style with dorsal arm acute apically; aedeagus with apical hook less developed, no process at base . . . . . . . . . . . . . . . . . . . . . . . . *strobila*, n. sp.
14(7). Style bifid apically; aedeagus with apical hook short; vertex with or without fuscous spots . . 15
— Styles not bifid apically or dorsal arm elongate; aedeagus with apical hook variable; vertex with or without fuscous spots . . . . . . . . . . 17
15(14). Aedeagus short, shaft serrate ventrally, widest at midlength; style without distinct lateral apical flange; vertex without fuscous spots . . . . . . . . . . . . . . . . . *supina* Ball & Beamer

— Aedeagus longer, shaft not serrate or widened; style variable; vertex with or without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . 16

16(15). Style with conspicuous apical lateral flange; vertex without fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *foeda* Ball & Beamer

— Style without apical lateral flange; vertex with fuscous spots . . . . . . . . . . . *parca* Ball & Beamer

17(14). Style with dorsal arm elongate; vertex without fuscous spots . . . . . . . . . *rostrata* Ball & Beamer

— Style without elongate dorsal arm; vertex usually with fuscous spots . . . . . . . . . . . . . . . . . . . 18

18(17). Aedeagus with shaft shortened, widest in apical 1/2, apical hook short; style with conspicuous lateral flange . . . . . . . . . . . . . . . . . . . . . . . 19

— Aedeagus with shaft longer, not widest in apical 1/2, apical hook longer; style without lateral flange . . . . . . . . . . . *fredonia* Ball & Beamer

19(18). Aedeagus with pronounced keels on ventral margin of shaft, shorter; hind tibial spur 1/2 1st tarsomere; from SW . . . . . . . . . *cursa*, n. sp.

— Aedeagus without pronounced keels on shaft, longer; hind tibial spur longer; from California (east face of Sierras) . . . . . . . *hemijona*, n. sp.

20(6). Style with apical dorsal arm truncate; vertex commonly with fuscous spots; plates rounded apically . . . . . . . . . . . . . . . *incerta* Ball & Beamer

— Style with apical dorsal arm rounded or acute; vertex usually without fuscous spots; plates variable . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

21(20). Plates rounded apically; style with ventral apical arm thickened, well developed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *kadokana* Knull

— Plates truncate apically; style with apical lateral flange; ventral apical arm not as well developed; vertex occasionally with fuscous spots . . . . . . . . . . . . . . . . . . *salsa* Ball & Beamer

22(5). Vertex usually without fuscous spots; aedeagus with serrated ventral margin; plates not elongate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 23

— Vertex usually with fuscous spots, or if absent, then aedeagus without ventral serrations; plates may be elongate . . . . . . . . . . . . . . . . . . 29

23(22). Style distinctly bifid apically; connective shorter than style; aedeagus without apical crests on shaft . . . . . . . . . . . . . . . . . . . . . . . . 25

— Style with only dorsal arm developed; connective variable in length; aedeagus with crests on shaft . . . . . . . . . . . . . . . . . . . . . . . . 24

24(23). Aedeagus with apical crests on shaft; connective equal to style in length; vertex occasionally with fuscous spots . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *kanabana* Ball & Beamer

— Aedeagus with medial crests on shaft; connective shorter than style; vertex without spots . . . . . . . . . . . . . . . . . . . . . . . . . . *furnaca*, n. sp.

25(23). Style with apical lateral flange, apical arms equal in length; aedeagus with shaft elongate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26

— Style without flange, dorsal arm longer; aedeagus with shaft shortened, acute apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27

26(25). Style with conspicuous lateral flange; plates short, truncate apically; vertex length less than interocular width . . . . . . . *marthae*, n. sp.

— Style with lateral flange smaller; plates rounded apically, vertex length may equal interocular width . . . . . . . . *bifida* Ball & Beamer

27(25). Style conspicuously bifid, dorsal arm slender, tapered . . . . . . . . . . . . . . . . . . . . . *utahna* Osborn

— Style less bifid, dorsal arm robust . . . . . . . . . 28

28(27). Style with dorsal arm acute apically; vertex occasionally with spots . . . . . . . *yumana* Osborn

— Style with dorsal arm bulbous apically; vertex without spots . . . . . . . . . . . . . . . . *deserta*, n. sp.

29(22). Tibial spur 2/3 length of 1st tarsomere; plates elongate, acute apically, exceeding apex of styles; outer arm of style acute apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *magdalena* Baker

— Tibial spur variable; plates shorter; style equal to or exceeding apex of plate, outer arm variable . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 30

30(29). Style with dorsal arm acute apically . . . . . . . . 31

— Style with dorsal arm rounded or truncate . . 32

31(30). Aedeagus with shaft approximately 1 1/2X length of dorsal apodeme, with minute serrations on ventral margin . . . *laeta* Ball & Beamer

— Aedeagus with shaft 2X length of dorsal apodeme, with conspicuous serrations on ventral margin . . . . . . . . . . . . . . . . *stylosa*, n. sp.

32(30). Style with outer arm rounded; aedeagus with shaft only slightly widened or tapered in apical 1/2, ventral margin with or without serrations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 33

— Style with outer arm truncate; aedeagus with shaft widest in apical 1/2, ventral margin not serrated . . . . . . . . . . . . . . . . . . *incongrua* Baker

33(32). Aedeagus with shaft short, widest at midlength; style with large lateral apical flange . . . . . . . . . . . . . . . . . . . . . . *tenera* Ball & Beamer

— Aedeagus with shaft longer, even-margined or slightly enlarged apically; style without conspicuous flange . . . . . . . . . . . . . . . . . . . . . 34

34(33). Style deeply bifid apically, ventral arm widened, dorsal arm even-margined; aedeagus with shaft slightly widened apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *vativala*, n. sp.

— Style less bifid, with inconspicuous apical lateral flange, dorsal arm tapered; aedeagus with shaft even-margined . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *terebrans* (Gillette & Baker)

## Characters Used in Character Code

Character 1. 0 = no fuscous spots on vertex.
1 = fuscous spots may be present.

Character 2. 0 = hind tibial spur 1/2 1st tarsomere or less.
1 = spur approximately length of 1st tarsomere.

Character 3. 0 = ocellus approximately its diameter from eye.
1 = ocellus more remote.
Character 4. 0 = male plates unicolorous.
1 = male plates embrowned apically.
Character 5. 0 = male plates elongate.
1 = male plates rounded apically.
2 = male plates truncate apically.
Character 6. 0 = male pygofer with caudal margin rounded.
1 = male pygofer with caudal margin extended.
Character 7. 0 = anal tube not reaching pygofer apex.
1 = anal tube equal to or exceeding pygofer apex.
Character 8. 0 = male pygofer not embrowned.
1 = male pygofer embrowned caudoventrally.
Character 9. 0 = male plates exceeding apex of pygofer.
1 = male plates equal to apex of pygofer.
2 = male plates not reaching apex of pygofer.
Character 10. 0 = styles not reaching apex of pygofer.
1 = styles equal to apex of pygofer.
2 = styles exceed apex of pygofer.
Character 11. 0 = styles not reaching apex of plates.
1 = styles equal to apex of plates.
2 = styles exceed apex of plates.
Character 12. 0 = styles without lateral flange.
1 = styles with lateral flange.
2 = styles with ventral arm thickened.
Character 13. 0 = connective shorter than style.
1 = connective as long as or longer than style.
Character 14. 0 = aedeagus with caudal surface smooth.
1 = aedeagus with caudal surface troughlike.
Character 15. 0 = shaft of aedeagus flared in caudal aspect.
1 = shaft even-margined in caudal aspect.
Character 16. 0 = aedeagus with no basal processes on shaft.
1 = shaft with basal processes.
Character 17. 0 = aedeagus with caudal margin of shaft smooth.
1 = caudal margin serrate.
Character 18. 0 = aedeagus with dorsal apodeme simple.
1 = dorsal apodeme enclosing shaft basally.

### *Athysanella gardenia* Osborn
Figs. 1–5

*Athysanella gardenia* Osborn 1930:701.
*Gladionura frigida* Osborn 1930:709.

Length of male 2.5 to 2.9 mm, female 3.2 to 3.4 mm; head width of male 1.0 to 1.05 mm, female 1.05 to 1.15 mm; pronotal width of male 0.95 to 1.05 mm, female 1.0 to 1.1 mm; interocular width of male 0.45 to 0.55 mm, female 0.5 to 0.55 mm; vertex length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm; pronotal length of male 0.3 to 0.4 mm, female 0.3 to 0.35 mm. Vertex length 0.76 to 0.8 interocular width; pronotal length 0.85 to 0.88 vertex length.

Character code: 1-1-1-1-2-0-0-0-2-1-2-0-0-1-0-0-0-0.

Lectotype, male (No. 43183), and lectoallotype, female (No. 43183), from Garden of the Gods, Colorado, (Webster) No. 7104, in USNM.

This species is related to *pastora* but can be distinguished by the apex of the style, which is narrowed (Fig. 2), and the posterior margin of the plate, which is embrowned and has a median projection. The style occasionally has macrosetae; long-winged specimens have been observed. This species has been collected in Colorado and Wyoming.

### *Athysanella robusta* Baker
Figs. 6–9

*Athysanella robusta* Baker 1898:187.
*Athysanella montana* Osborn 1930:700.

Length of male 2.3 to 3.1 mm, female 3.4 to 3.7 mm; head width of male 0.95 to 1.15 mm, female 1.05 to 1.15 mm; pronotal width of male 0.9 to 1.15 mm, female 1.05 to 1.15 mm; interocular width of male 0.4 to 0.55 mm, female 0.5 to 0.55 mm; vertex length of male 0.35 to 0.5 mm, female 0.4 to 0.5 mm; pronotal length of male 0.3 to 0.4 mm, female 0.35 to 0.4 mm. Vertex length 0.8 to 0.9 interocular width; pronotal length 0.76 to 0.88 vertex width.

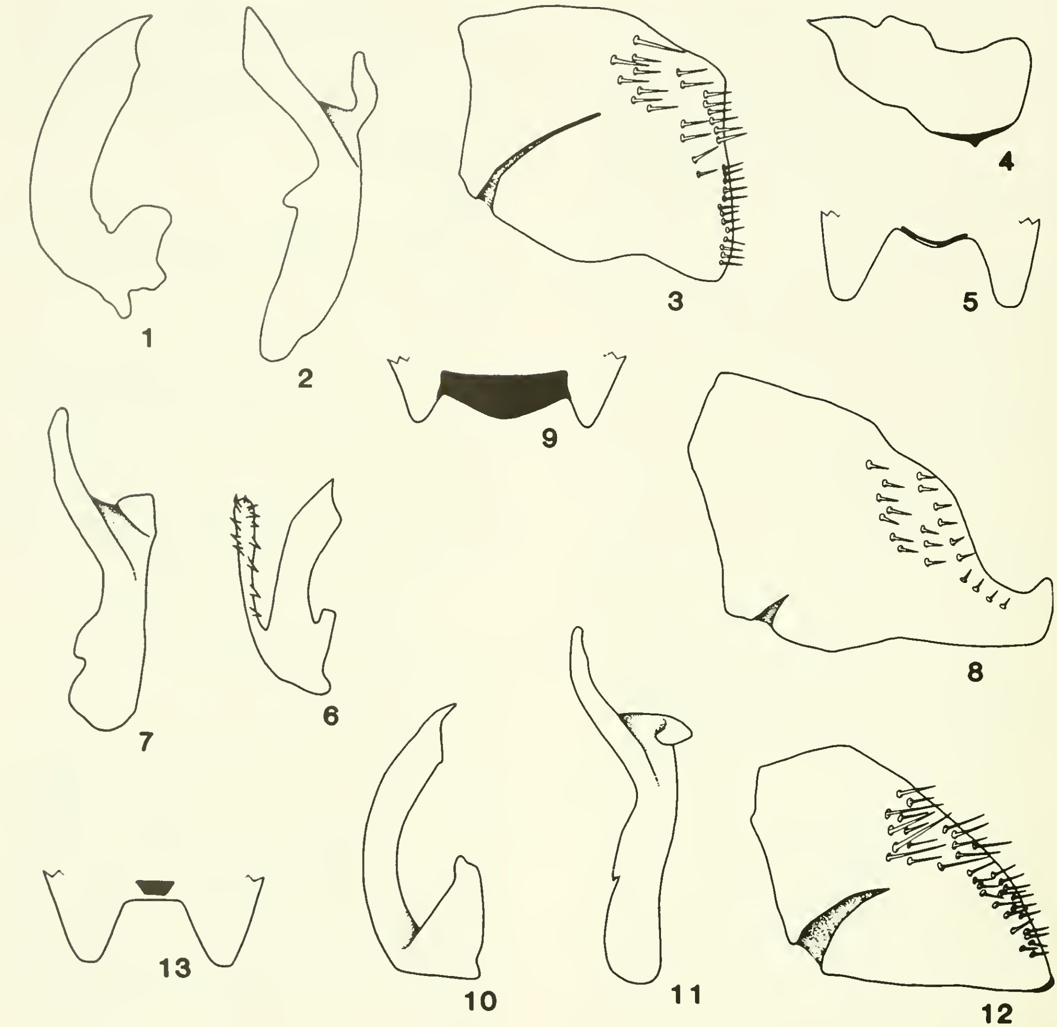
Character code: 0-0-1-1-2-1-1-0-2-0-2-0-1-0-0-1-0-0.

The type of this species has not been studied; identification is based on determined material from various collections and the literature.

*Athysanella robusta* is related to *pastora* but can be separated by the unique shape of the aedeagus (Fig. 6), the pronotum nearly as wide as the head, and the connective, which is as long as the style. There are no fuscous spots on the vertex of this species. It has been collected in Colorado, Montana, Nebraska, North Dakota, Wyoming, and Canada.

### *Athysanella pastora* Blocker, n. sp.
Figs. 10–13

Length of male 2.5 to 2.7 mm, female 3.6 to




Figs. 1–13. Figs. 1–5. *Athysanella gardenia:* 1, aedeagus, lateral view; 2, style, broad aspect; 3, pygofer, lateral view; 4, plate, ventral view; 5, female sternum VII, ventral view. Figs. 6–9. *Athysanella robusta:* 6, aedeagus, lateral view; 7, style, broad aspect; 8, pygofer, lateral view; 9, female sternum VII, ventral view. Figs. 10–13. *Athysanella pastora:* 10, aedeagus, lateral view; 11, style, broad aspect; 12, pygofer, lateral view; 13, female sternum VII, ventral view.

3.9 mm; head width of male 1.05 to 1.15 mm, female 1.2 to 1.25 mm; pronotal width of male 0.9 to 1.0 mm, female 1.05 to 1.15 mm; interocular width of male 0.4 to 0.5 mm, female 0.5 to 0.6 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.4 mm, female 0.35 to 0.4 mm. Vertex length 0.84 to 0.95 interocular width; pronotal length 0.76 to 0.94 vertex length.

Character code: 1-1-0-1-1-1-0-1-1-2-2-0-0-0-0-0-0-0.

Color stramineous; vertex with fuscous spots; vertex, pronotum, and abdomen with additional, conspicuous brown pattern; forewings commonly with darkened stripes; face with lateral fuscous marks; legs with various amounts of fuscous coloring.

Forewings brachypterous, exposing 3 to 4 pregenital abdominal terga; ocellus approximately 1.5 its diameter from eye; hind tibial spur 3/4 length of 1st tarsomere; female abdominal sternum VII (Fig. 13) variable but hind margin usually with conspicuous lateral lobes, medial third truncate or rounded, variously embrowned.

Pygofer with caudal margin extended, slightly embrowned on caudoventral border, densely set with macrosetae (25+); anal tube attains apex of pygofer; valve with caudal margin rounded; plates rounded and conspicuously embrowned apically, slightly separated at base; connective 2/3 or less length of style; styles rounded apically, with conspicuous preapical lobe, apex slightly exceeding apex of plates; aedeagus with shaft simple, slightly enlarged apically, elongate, with dorsal apodeme slightly overlapping base of shaft.

Holotype, male, from Chaves Co., New Mexico, Bitter Lake NWR, 14 Aug 1984 (R. F. Whitcomb); 4 male and 8 female paratypes, same data. Holotype and paratypes in USNM; paratypes in IPL and KSU.

*Athysanella pastora* is related to *robusta* and *globosa* but can be separated from the former by the absence of an aedeagal process. It can be separated from *globosa* by the shape of the apex of the style, which is not widened (Fig. 11), and by the shaft of the aedeagus (Fig. 10), which is elongate and not serrated. This species has been collected only on gyp grama, *Bouteloua breviseta*, in gypsum flats of southeastern New Mexico.

### *Athysanella globosa* Ball & Beamer
Figs. 14–15

*Athysanella globosa* Ball & Beamer 1940:18.

Length of male 2.9 mm; head width 1.2 mm; pronotal width 1.1 mm; interocular width 0.45 mm; vertex length 0.35 mm; pronotal length 0.4 mm. Vertex length 0.78 interocular width; pronotal length 1.07 vertex length. Female unknown.

Character code: 1-0-1-1-2-1-1-0-1-1-1-0-0-1-0-0-1-0.

Holotype, male, from Grand Canyon, Arizona, 4 Aug 1930 (E. D. Ball) in USNM. Male and female paratypes, same data, at KU.

*Athysanella globosa* is related to *gardenia* but can be separated by the shape of the shaft of the aedeagus, which is serrate at midlength (Fig. 14). Female paratypes examined are doubtfully conspecific with the male. This species is known only from its type locality in Arizona; a specimen from Utah is assigned to this species but may represent a new species.

### *Athysanella planata* Ball & Beamer
Figs. 16–18

*Athysanella planata* Ball & Beamer 1940:24.

Length of male 2.6 to 2.7 mm, female 3.4 to 4.0 mm; head width of male 1.0 to 1.05 mm, female 1.1 to 1.15 mm; pronotal width of male 0.9 to 1.0 mm, female 1.0 to 1.1 mm; interocular width of male 0.35 to 0.4 mm, female 0.4 to 0.5 mm; vertex length of male 0.35 mm to 0.4 mm, female 0.4 to 0.45 mm; pronotal length of male 0.3 to 0.35 mm, female 0.3 to 0.35 mm. Vertex length 0.87 to 1.0 interocular width; pronotal length 0.8 to 0.86 vertex length.

Character code: 0-1-0-0-1-0-0-0-1-1-1-2-0-0-0-0-0-0.

Holotype, male, and allotype, female, from Newberry Springs, California, 30 July 1936 (D. R. Lindsay and R. H. Beamer) in KU.

*Athysanella planata* is related to *krameri* but can be separated by the presence of processes on the base of the shaft of the aedeagus (Fig. 16), a more slender apical arm of the style (Fig. 17), and the absence of fuscous spots on the vertex. This species has been collected only from the type locality in California.

### *Athysanella krameri* Blocker, n. sp.
Figs. 19–21

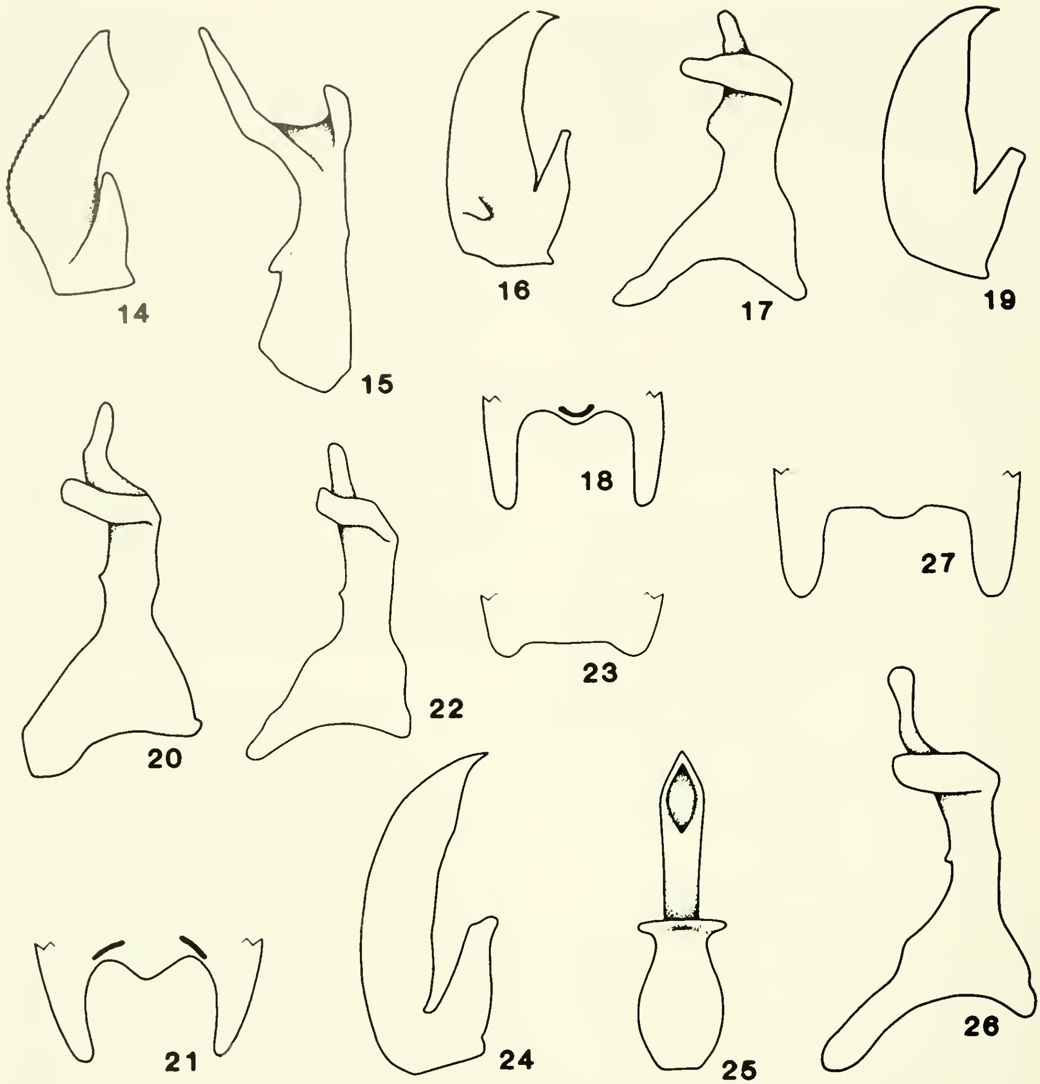
Length of male 3.0 to 3.1 mm, female 4.4 to 4.7 mm; head width of male 1.05 to 1.15 mm, female 1.2 to 1.25 mm; pronotal width of male 1.0 to 1.1 mm, female 1.1 to 1.2 mm; interocular width of male 0.45 to 0.5 mm, female 0.55 to 0.6 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.83 to 0.95 interocular width; pronotal length 0.77 to 0.87 vertex length.

Character code: 1-1-0-0-1-1-0-0-2-1-2-0-0-0-0-0-0-0 .

Color stramineous; vertex commonly with fuscous spots, often with orange dashes; male pygofer commonly with conspicuous fuscous spot; remainder of body mostly unicolorous; female without fuscous spots on vertex.

Forewings brachypterous, exposing 3.5 to 4.5 pregenital abdominal terga; ocellus 1.5 its diameter (or less) from eye; hind tibial spur approximately 3/4 length of 1st tarsomere; female abdominal sternum VII (Fig. 21) with elongate lateral lobes and rounded medial lobe on hind margin.

Pygofer rounded apically, with about 20 macrosetae; valve rounded on apical margin; plates rounded apically, slightly separated or touching at base; connective less than 3/4




Figs. 14–27. Figs. 14–15. *Athysanella globosa:* 14, aedeagus, lateral view; 15, style, broad aspect. Figs. 16–18. *Athysanella planata:* 16, aedeagus, lateral view; 17, style, broad aspect; 18, female sternum VII, ventral view. Figs. 19–21. *Athysanella krameri:* 19, aedeagus, lateral aspect; 20, style, broad aspect; 21, female sternum VII, ventral aspect. Figs. 22–23. *Athysanella whitcombi:* 22, style, broad aspect; 23, female sternum VII, ventral view. Figs. 24–27. *Athysanella plana:* 24, aedeagus, lateral view; 25, aedeagus, anterodorsal view; 26, style, broad aspect; 27, female sternum VII, ventral view.

length of style; styles (Fig. 20) bifid apically, dorsal arm short, robust, no preapical lobe, exceeding apex of plates, equal to apex of pygofer; aedeagus (Fig. 19) with shaft short, widest basally, and tapered to acute apical hook.

Holotype, male, from Little Lake, Inyo Co., California, 7 June 1929 (E. P. Van Duzee); 5 male and 6 female paratypes, same data; 3 males from Olancha, Inyo Co., 8 June 1929; 1 male from Lone Pine, Inyo Co., 10 June 1929. Holotype and paratypes in CAS, paratypes in KSU.

*Athysanella krameri* is related to *planata* but can be separated by the absence of projections at the base of the aedeagus and the dorsal arm of the style, which is shorter and more robust. An undeveloped male specimen has

been observed. This species is known only from the above localities in California.

*Athysanella whitcombi* Blocker, n. sp.
Figs. 22–23

Length of male 2.6 mm, female 4.0 mm; head width of male 1.0 mm, female 1.15 to 1.2 mm; pronotal width of male 0.9 mm, female 1.0 to 1.05 mm; interocular width of male 0.4 mm, female 0.55 to 0.6 mm; vertex length of male 0.35 to 0.4 mm, female 0.5 mm; pronotal length of male 0.25 to 0.3 mm, female 0.45 mm. Vertex length 0.93 to 0.94 interocular width; pronotal length 0.73 to 0.74 vertex length.

Character code: 0-1-1-0-1-0-0-0-1-1-1-1-0-0-0-0-0-1.

Color stramineous; vertex without fuscous spots; body virtually unicolorous.

Forewings of male brachypterous, exposing 4.5 pregenital abdominal terga; ocellus approximately 2X its diameter from eye; hind tibial spur about 1/2 length of 1st tarsomere; female abdominal sternum VII with lateral lobes, without medial lobe on caudal margin.

Pygofer rounded, with about 20 macrosetae; valve rounded on caudal margin; plates rounded apically, touching at base then divergent apically; connective 3/4 length of style; styles bifid apically, dorsal arm slender, no preapical lobe, exceeding apex of plates, equal to apex of pygofer; aedeagus with shaft and dorsal apodeme as *plana*.

Holotype, male, from Austin, Nevada, 12 Aug 1940 (D. E. Hardy) and a long-winged female paratype, same data, in KU.

*Athysanella whitcombi* is related to *plana* but can be separated by its smaller size, the absence of fuscous spots on the vertex, and the more slender dorsal apical arm of the style. This species is named for R. F. Whitcomb, who has made numerous contributions to this research; it has been collected in Nevada.

*Athysanella plana* Ball & Beamer
Figs. 24–27

*Athysanella plana* Ball & Beamer 1940:13.

Length of male 3.0 to 3.3 mm, female 4.5 to 4.7 mm; head width of male 1.05 to 1.15 mm, female 1.2 to 1.25 mm; pronotal width of male 1.0 to 1.05 mm, female 1.15 to 1.2 mm; interocular width of male 0.45 to 0.5 mm, female 0.55 to 0.6 mm; vertex length of male 0.4 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.4 mm, female 0.35 to 0.4 mm. Vertex length 0.89 to 0.95 interocular width; pronotal length 0.77 to 0.82 vertex length.

Character code: 1-1-1-0-2-0-0-0-1-1-1-1-0-0-0-0-0-0.

Holotype, male, and allotype, female, from Califa, California, 12 June 1935 (P. W. Oman) in USNM; paratypes in USNM.

*Athysanella plana* is related to *aspera* but can be separated by the expanded base of the dorsal apodeme of the aedeagus (Fig. 25) and the longer dorsal apical arm of the style (Fig. 26). This species has been collected only from the Central Valley (Fresno Co.) of California.

*Athysanella aspera* Ball & Beamer
Figs. 28–30

*Athysanella aspera* Ball & Beamer 1940:17.

Length of male 2.5 to 3.1 mm, female 4.3 to 5.0 mm; head width of male 0.95 to 1.15 mm, female 1.15 to 1.3 mm; pronotal width of male 0.9 to 1.1 mm, female 1.1 to 1.25 mm; interocular width of male 0.4 to 0.5 mm, female 0.45 to 0.5 mm; vertex length of male 0.35 to 0.45 mm, female 0.4 to 0.5 mm; pronotal length of male 0.3 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.8 to 0.95 interocular width; pronotal length 0.76 to 0.93 vertex length.

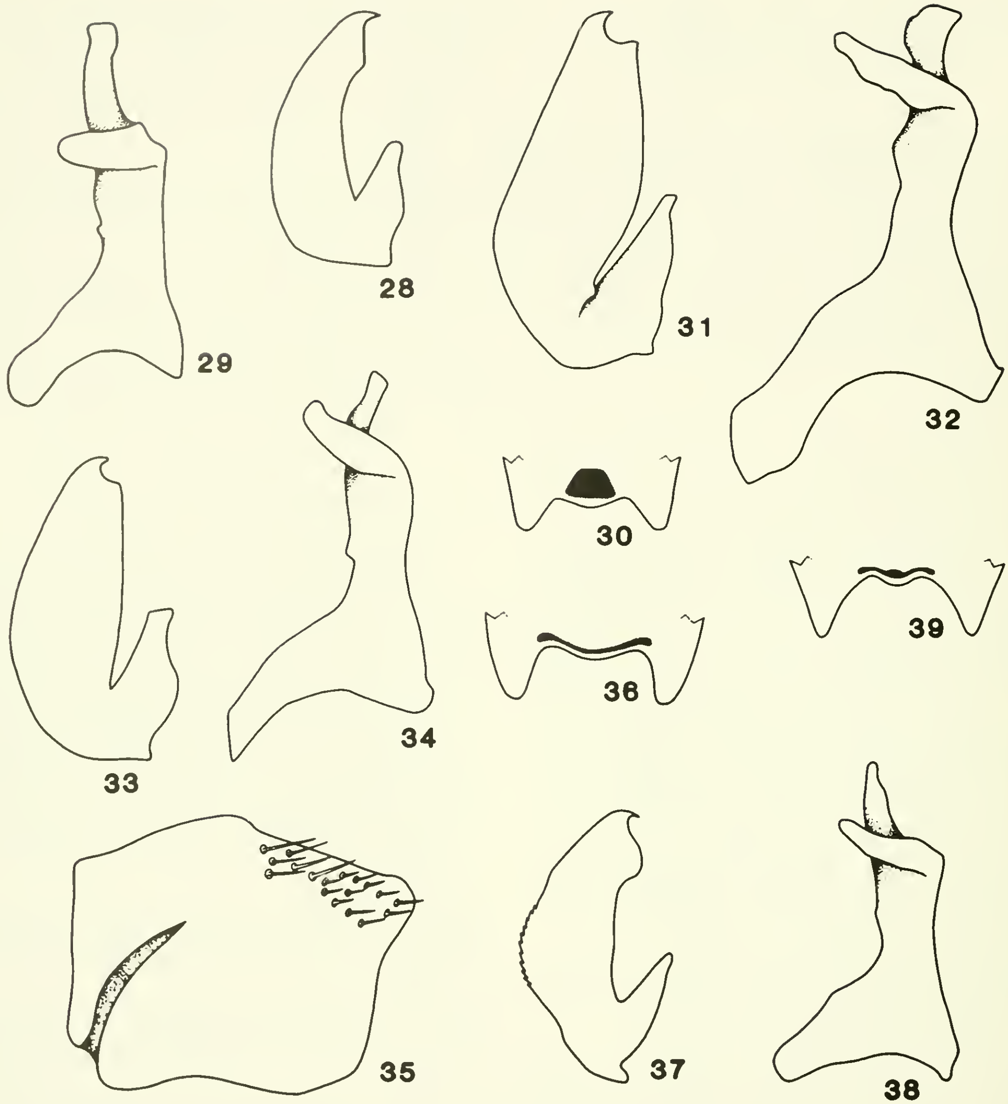
Character code: 1-1-1-0-2-1-0-0-2-1-2-1-0-0-0-0-0-0.

Holotype, male, and allotype, female, from Mojave, California, 1 July 1931 (E. D. Ball) in USNM.

*Athysanella aspera* is related to *plana* but can be separated by the apex of the style, which has a shorter dorsal arm (Fig. 29), and the dorsal apodeme of the aedeagus, which is not widened apically. In one specimen, the vertex length equaled the interocular width. The shaft of the aedeagus has an indistinct pair of basal tubercles similar to *planata*. A male specimen parasitized by Pipinculidae and specimens with undeveloped genitalia have been observed. This species has been collected from the Mojave Desert in California.

*Athysanella aphoda* Blocker, n. sp.
Figs. 31–32

Length of male 3.5 mm; head width 1.2 mm; pronotal width 1.1 mm; interocular width 0.5 mm; vertex length 0.45 mm; pronotal length 0.4 mm; female unknown. Vertex 0.9 interocular width; pronotal length 0.83 to




Figs. 28–39. Figs. 28–30. *Athysanella aspera:* 28, aedeagus, lateral view; 29, style, broad aspect; 30, female sternum VII, ventral view. Figs. 31–32. *Athysanella aphoda:* 31, aedeagus, lateral view; 32, style, broad aspect. Figs. 33–36. *Athysanella strobila:* 33, aedeagus, lateral view; 34, style, broad aspect; 35, pygofer, lateral aspect; 36, female sternum VII, ventral view. Figs. 37–39. *Athysanella supina:* 37, aedeagus, lateral view; 38, style, broad aspect; 39, female sternum VII, ventral view.

0.84 vertex length. Female unknown.

Character code: 1-0-1-0-2-0-1-0-2-1-2-2-0-0-0-1-0-0.

Color stramineous; vertex and pronotum with distinct, darker pattern; forewings with dark stripes; face with distinct lateral arcs; legs with slight fuscous coloring.

Forewings brachypterous, exposing 3.5 pregenital abdominal terga; ocellus approximately its diameter from eye; hind tibial spur slightly shorter than 1st tarsomere.

Pygofer as *strobila* but larger; valve rounded posteriorly; plates truncate apically; styles (Fig. 32) with dorsal arm bulbous apically; aedeagus (Fig. 31) with apical hook more distinct than *strobila*, shaft with indistinct, small process at base.

Holotype, male, from Lander Co., Nevada,

30 mi N Austin, 24 July 1986 (H. D. Blocker) in KSU.

*Athysanella aphoda* is closely related to and possibly conspecific with *strobila* but can be readily separated by its larger size, the bulbous apex of the dorsal arm of the style, and the more robust aedeagus, which has a more pronounced apical hook. This species is represented by the holotype from Nevada.

### *Athysanella strobila* Blocker, n. sp.
Figs. 33–36

Length of male 2.6 to 3.9 mm, female 4.2 to 5.3 mm; head width of male 1.05 to 1.3 mm, female 1.15 to 1.35 mm; pronotal width of male 0.95 to 1.25 mm, female 1.05 to 1.3 mm; interocular width of male 0.4 to 0.55 mm, female 0.45 to 0.65 mm; vertex length of male 0.4 to 0.55 mm, female 0.45 to 0.65 mm; pronotal length of male 0.3 to 0.4 mm, female 0.3 to 0.45 mm. Vertex length 0.89 to 1.0 interocular width; pronotal length 0.7 to 0.82 vertex length.

Character code: 0-1-0-0-2-0-0-0-2-1-2-2-0-1-0-0-0-0.

Color stramineous, occasionally patterned; vertex without fuscous spots; abdomen occasionally with some darker pattern; other body areas occasionally with irregular, brown pattern.

Forewings brachypterous, exposing 3.0 to 4.5 pregenital abdominal terga; ocellus approximately its diameter from eye; hind tibial spur 3/4 length of 1st tarsomere; female abdominal sternum VII (Fig. 36) with conspicuous lateral lobes on posterior margin, with a broadly rounded medial lobe.

Pygofer rounded on caudoventral margin, with a distinct lobe (Fig. 35), with 15 or fewer macrosetae; valve rounded posteriorly; plates truncate apically, nearly touching basally, then diverging; connective 3/4 length of style; styles bifid (Fig. 34) apically, with ventral arm thickened, exceeding apex of plates, equal to apex of pygofer; aedeagus with shaft short, widest in proximal 1/2, slightly tapered in apical 1/2 to a single apical hook.

Holotype, male, from Lone Pine, California, 28 July 1940 (R. H. Beamer); 4 male and 3 female paratypes, same data; male and female, Fallon, Nevada, 12 Aug 1940 (L. C. Kuitert); 2 males and 8 females, New Humboldt Co., Nevada, 7 mi W Denio, 23 June 1971 (Oman); 6 males and 3 females, Eureka Co., Nevada, W. Eureka, 25 July, 1986 (H. D. Blocker); male and female, Lander Co., Nevada, 5 mi W Austin, 24 July 1986 (H. D. Blocker); male, Owyhee Co., Idaho, 10 mi W Bruneau, 9 July 1981 (H. D. Blocker, J. W. Johnson); numerous specimens from Albert Lake, Oregon, 5 mi N Valley Falls, 18 May 1969 (Oman), and 6 mi N Silver Lake, Oregon, 17 May 1969 (Oman). Holotype and paratypes in KU; paratypes in KSU and OrSU.

*Athysanella strobila* is closely related to *aspera* but can be separated by the shape of the shaft of the aedeagus, which is more robust and shorter, and by the dorsal apical arm of the style, which is longer and acute apically. It can be recognized by the unique lobe on the caudal margin of the pygofer. An undeveloped female specimen has been examined. This species has been collected in California, Idaho, Nevada, and Oregon.

### *Athysanella supina* Ball & Beamer
Figs. 37–39

*Athysanella supina* Ball & Beamer 1940:22.

Length of male 2.8 to 3.2 mm, female 4.3 to 4.6 mm; head width of male 1.0 to 1.1 mm, female 1.15 to 1.25 mm; pronotal width of male 1.0 to 1.05 mm, female 1.1 to 1.2 mm; interocular width of male 0.45 to 0.5 mm, female 0.55 to 0.6 mm; vertex length of male 0.45 to 0.55 mm, female 0.5 to 0.6 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 1.0 to 1.15 interocular width; pronotal length 0.68 to 0.75 vertex length.

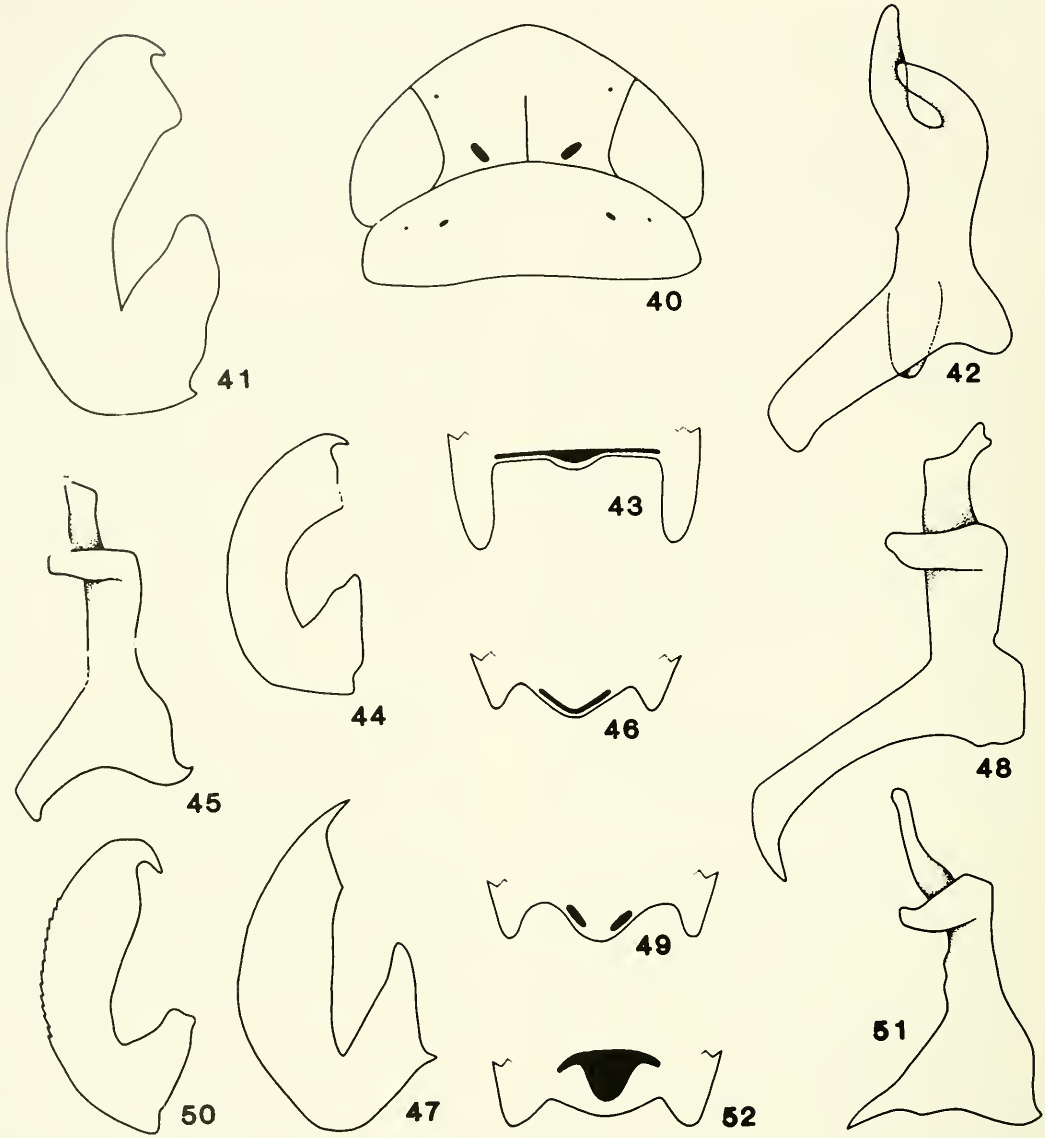
Character code: 1-1-1-0-1-0-0-0-2-1-2-1-0-1-0-0-1-0.

Holotype, male, and allotype, female, from Boca Chica, Texas, 30 May 1933 (P. W. Oman) in USNM; paratypes in USNM and KU.

*Athysanella supina* is related to *fredonia* but can be separated by the shaft of the aedeagus, which has a shorter crest on the ventral margin (Fig. 37), and the shape of the apex of the style, which is more bifid (Fig. 38). This species, described from Texas, has recently been collected there (A. L. Hicks) from shoregrass, *Monathochloe littoralis*.

### *Athysanella foeda* Ball & Beamer
Figs. 40–43

*Athysanella foeda* Ball & Beamer 1940:19.




Figs. 40–52. Figs. 40–43. *Athysanella foeda:* 40, head and prothorax, dorsal view; 41, aedeagus, lateral view; 42, style, broad aspect; 43, female sternum VII, ventral view. Figs. 44–46. *Athysanella parca:* 44, aedeagus, lateral view; 45, style, broad aspect; 46, female sternum VII, ventral view. Figs. 47–49. *Athysanella rostrata:* 47, aedeagus, lateral view; 48, style, broad aspect; 49, female sternum VII, ventral aspect. Figs. 50–52. *Athysanella fredonia:* 50, aedeagus, lateral view; 51, style, broad aspect; 52, female sternum VII, ventral view.

Length of male 3.4 to 3.6 mm, female 4.9 to 5.1 mm; head width of male 1.2 to 1.3 mm, female 1.4 to 1.5 mm; pronotal width of male 1.2 to 1.3 mm, female 1.35 to 1.4 mm; interocular width of male 0.55 to 0.6 mm, female 0.65 to 0.75 mm; vertex length of male 0.5 to 0.55 mm, female 0.55 to 0.6 mm; pronotal length of male 0.4 to 0.45 mm, female 0.4 to 0.45 mm. Vertex length 0.83 to 0.88 interocular width; pronotal length 0.76 to 0.85 vertex length.

Character code: 0-1-1-0-1-0-0-0-1-2-2-1-0-1-0-0-0-1.

Holotype, male, and allotype, female, from Laramie, Wyoming, 23 June 1935 (R. H. and

J. Beamer) in KU; paratypes in KU.

*Athysanella foeda* is related to *parca* but can be separated by its larger size and the presence of a conspicuous lateral lobe at the apex of the style (Fig. 42). It can be separated from *fredonia* by the shape of the apex of the style, which is distinctly bifid. This species has been collected in Wyoming.

### *Athysanella parca* Ball & Beamer
Figs. 44–46

*Athysanella parca* Ball & Beamer 1940:15.

Length of male 2.7 to 3.4 mm, female 3.9 to 4.4 mm; head width of male 1.0 to 1.15 mm, female 1.15 to 1.4 mm; pronotal width of male 0.9 to 1.15 mm, female 1.05 to 1.25 mm; interocular width of male 0.4 to 0.5 mm, female 0.5 to 0.65 mm; vertex length of male 0.4 to 0.45 mm, female 0.45 to 0.55 mm; pronotal length of male 0.3 to 0.4 mm, female 0.4 to 0.45 mm. Vertex length 0.89 to 0.95 interocular width; pronotal length 0.82 to 0.88 vertex length.

Character code: 1-1-0-0-1-0-0-0-2-1-2-2-0-0-0-0-0-0.

Holotype, male, and allotype, female, from Belen, New Mexico, 20 July 1936 (R. H. Beamer and D. R. Lindsay) in KU; paratypes in KU.

*Athysanella parca* is related to *foeda* but can be separated by the absence of a lateral flange on the style and the usual presence of fuscous spots on the vertex. It can be separated from *incerta* by the shape of the apex of the shaft of the aedeagus, which has a single acute apical hook (Fig. 44). A long-winged female has been examined. This species has been collected in Colorado and New Mexico; in New Mexico, the host is saltgrass, *Distichlis stricta*.

### *Athysanella rostrata* Ball & Beamer
Figs. 47–49

*Athysanella rostrata* Ball & Beamer 1940:21.

Length of male 3.5 mm, female 5.0 to 5.1 mm; head width of male 1.15 to 1.25 mm, female 1.3 to 1.35 mm; pronotal width of male 1.1 to 1.15 mm, female 1.2 to 1.25 mm; interocular width of male 0.5 to 0.55 mm, female 0.6 to 0.65 mm; vertex length of male 0.45 to 0.5 mm, female 0.5 to 0.55 mm; pronotal length of male 0.35 to 0.4 mm, female 0.4 to 0.45 mm. Vertex length 0.86 to 0.91 interocular width; pronotal length 0.75 to 0.78 vertex length.

Character code: 0-1-0-0-2-0-0-0-2-2-2-2-0-1-0-0-0-0.

Holotype, male, and allotype, female, from Perris, California, 5 June 1935 (P. W. Oman) in USNM; paratypes in USNM.

*Athysanella rostrata* is related to *foeda* but can be separated by the distinctly elongate dorsal arm of the style (Fig. 48). A paratype with undeveloped genitalia has been examined. This species has been collected only from its type locality in southern California.

### *Athysanella fredonia* Ball & Beamer
Figs. 50–52

*Athysanella fredonia* Ball and Beamer, 1940:12 (in part).

Length of male 2.6 to 2.9 mm, female 3.9 to 4.3 mm; head width of male 1.0 to 1.15 mm, female 1.15 to 1.4 mm; pronotal width of male 0.95 to 1.1 mm, female 1.0 to 1.25 mm; interocular width of male 0.4 to 0.45 mm, female 0.45 to 0.6 mm; vertex length of male 0.35 to 0.4 mm, female 0.4 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.83 to 0.94 interocular width; pronotal length 0.75 to 0.87 vertex length.

Character code: 1-1-0-0-1-0-0-0-1-1-1-0-0-1-0-0-1-0.

Color stramineous; vertex with fuscous spots anteriorly; pronotum commonly with small brown spots; other dorsal body pattern variable; face with lateral fuscous marks; legs with various amounts of fuscous coloring.

Forewings brachypterous, exposing 3.5 to 4.0 pregenital abdominal terga; ocellus approximately its diameter from eye; hind tibial spur over 3/4 length of 1st tarsomere; female abdominal sternum VII (Fig. 52) with lateral lobes extending posteriorly slightly more than median lobe.

Pygofer rounded apically, densely set with short setae; valve rounded on apical margin; plates rounded apically, slightly separated at base; connective shorter than style; styles (Fig. 51) widened apically, nearly truncate, dorsal arm acute apically, curved, usually with conspicuous lateral flange, equal to apex of plates and pygofer; aedeagus (Fig. 50) with shaft not widened apically, finely serrate on ventral margin.

Holotype, male, from Fredonia, Arizona, 6 Aug 1930 (E. D. Ball) in USNM.

*Athysanella fredonia* is related to *cursa* but can be separated by the longer shaft of the aedeagus, which is not widened apically. Examination of the holotype has revealed that the male genitalia differ from the genitalia described by Ball and Beamer (1940). For this reason, *fredonia* is redescribed and a new species, *cursa*, which agrees with the published illustration, is described. It has been collected in Arizona, Colorado, New Mexico, Nevada, and Utah, where it occurs on galleta, *Hilaria jamesii*. At the type locality, it occurs with *cursa* on the same host (R. F. Whitcomb).

### *Athysanella cursa* Blocker, n. sp.

Figs. 53–55

*Athysanella fredonia* Ball & Beamer (in part).

Length of male 2.5 to 3.0 mm, female 4.0 to 4.4 mm; head width of male 1.05 to 1.15 mm, female 1.2 to 1.3 mm; pronotal width of male 0.95 to 1.05 mm, female 1.1 to 1.2 mm; interocular width of male 0.4 to 0.45 mm, female 0.5 to 0.6 mm; vertex length of male 0.35 to 0.4 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.88 to 0.94 interocular width; pronotal length 0.8 to 0.88 vertex length.

Character code: 0-1-0-0-1-0-0-0-1-1-1-1-0-1-0-0-1-0.

Color stramineous with fuscous spots on vertex; vertex, pronotum, and abdomen variously patterned with brown markings; forewings commonly with brown stripes; face with lateral fuscous marks, legs with various amounts of fuscous coloring.

Forewings brachypterous, exposing 3.5 to 4.5 pregenital abdominal sterna; ocellus approximately 1.5X its diameter from eye; hind tibial spur usually about 1/2 length of 1st tarsomere; female abdominal sternum VII (Fig. 55) with lateral lobes slightly longer than median lobe.

Pygofer rounded but slightly extended apically; densely set with short setae; valve with caudal margin rounded; plates rounded apically; connective shorter than styles; styles (Fig. 54) widened apically and shallowly bifid, dorsal arm narrowed and acute apically, usually with a conspicuous lateral flange, equal to apex of plates and pygofer; aedeagus (Fig. 53) with shaft short, lightly serrate on ventral margin, with pronounced flanges on ventral margin, slightly widest in apical 1/2.

Holotype, male, from Whites City, New Mexico, 13 July 1936 (R. H. Beamer). One male and two female paratypes from Flagstaff, Arizona, 27 July 1936 (R. H. Beamer); two males from Flagstaff, Arizona, 21 July 1936 (D. R. Lindsey); female from St. Johns, Arizona, 26 July 1936 (R. H. Beamer); two males from Estancia, New Mexico, 24 June 1940 (R. H. Beamer); five males and one female from Cuervo, New Mexico, 23 June 1940 (R. H. Beamer). Holotype in KU; paratypes in KU and KSU.

*Athysanella cursa* is closely related to *hemijona* but can be separated by the shorter aedeagus with pronounced flanges on the ventral margin, the shorter tibial spurs, and the pygofer, which is slightly extended apically. The plates occasionally have a macroseta. Long-winged specimens and specimens parasitized by Dryinidae have been observed. This species is illustrated as *fredonia* in Ball and Beamer (1940), but a study of the holotype of *fredonia* reveals that this is a different species. It has been reported from the Desert Plains region of Arizona, Colorado, New Mexico, and Utah, where it occurs on galleta, *Hilaria jamesii*.

### *Athysanella hemijona* Blocker, n. sp.

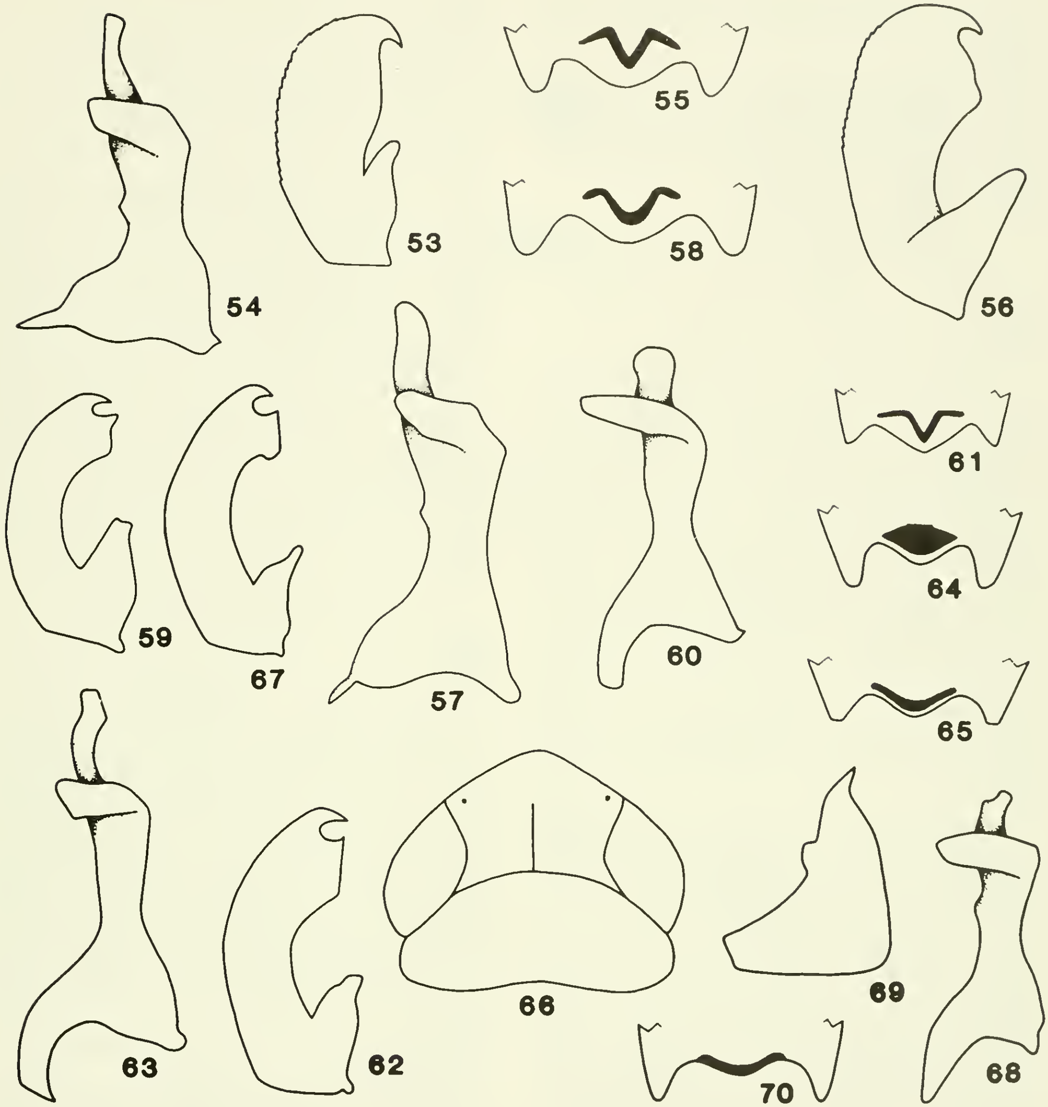
Figs. 56–58

Length of male 3.2 to 3.3 mm, female 4.8 to 4.9 mm; head width of male 1.2 to 1.25 mm, female 1.3 to 1.4 mm; pronotal width of male 1.1 to 1.15 mm, female 1.25 to 1.3 mm; interocular width of male 0.45 to 0.55 mm, female 0.5 to 0.55 mm; vertex length of male 0.4 to 0.45 mm, female 0.5 to 0.55 mm; pronotal length of male 0.35 to 0.4 mm, female 0.4 to 0.45 mm. Vertex length 0.85 to 0.95 interocular width; pronotal length 0.73 to 0.83 vertex length.

Character code: 1-1-0-0-1-0-0-0-1-1-1-1-0-1-0-0-1-1.

Color stramineous; vertex with fuscous spots; vertex, pronotum, and abdomen with conspicuous, dark pattern; forewings with darkened stripes; face with lateral fuscous marks; legs with various amounts of fuscous coloring.

Forewings brachypterous, exposing 3.5 to 4.5 pregenital abdominal terga; ocellus approximately 1.5X its diameter from eye; hind tibial spur over 3/4 length of 1st tarsomere; female abdominal sternum VII (Fig. 58) with




Figs. 53–70. Figs. 53–55. *Athysanella cursa:* 53, aedeagus, lateral view; 54, style, broad aspect; 55, female sternum VII, ventral view. Figs. 56–58. *Athysanella hemijona:* 56, aedeagus, lateral view; 57, style, broad aspect; 58, female sternum VII, ventral view. Figs. 59–61. *Athysanella incerta:* 59, aedeagus, lateral view; 60, style, broad aspect; 61, female sternum VII, ventral view. Figs. 62–65. *Athysanella kadokana:* 62, aedeagus, lateral view; 63, style, broad aspect; 64, 65, female sternum VII, ventral view. Figs. 66–70. *Athysanella salsa:* 66, head and pronotum, dorsal view; 67, aedeagus, lateral view; 68, style, broad aspect; 69, male plate, ventral view; 70, female sternum VII, ventral view.

median lobe approximately same length as lateral lobes.

Pygofer rounded apically, densely set with short, stubby setae; valve with caudal margin broadly rounded; plates broadly rounded, slightly separated at base; connective shorter than style; styles (Fig. 57) widened apically, shallowly bifid, dorsal arm constricted and curved; preapical lobe inconspicuous, with conspicuous apical lateral lobe, extending to apex of plates and pygofer; aedeagus (Fig. 56) with shaft short, slightly wider apically, serrated on ventral margin.

Holotype, male, from Inyo Co., California, Westgard Pass, 14 June 1983, sweeping grasses (R. J. Gill and D. Blocker). Two male

and three female paratypes, same data. Holotype and paratype in KSU; paratypes in CDA and KU.

*Athysanella hemijona* is related to *cursa* but can be separated by the shaft of the aedeagus, which is longer, and with the ventral margin not as flared. This species is known only from its type locality in California.

### *Athysanella incerta* Ball & Beamer
Figs. 59–61

*Athysanella incerta* Ball & Beamer 1940:15.

Length of male 2.7 to 3.3 mm, female 3.9 to 4.1 mm; head width of male 1.05 to 1.1 mm, female 1.1 to 1.25 mm; pronotal width of male 1.0 to 1.1 mm; female 1.0 to 1.15 mm; interocular width of male 0.45 to 0.5 mm, female 0.5 to 0.55 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.84 to 0.95 interocular width; pronotal length 0.75 to 0.82 vertex length.

Character code: 1-1-0-0-1-0-0-0-2-1-2-2-0-0-0-0-0-0.

Holotype, male, and allotype, female, from Lamar, Colorado, 20 Aug 1936 (R. H. Beamer) in KU; paratypes in KU, USNM, and CSU.

*Athysanella incerta* is very closely related to *kadokana* but can be separated by the shape of the apex of the style (Fig. 60), which is not excavated as deeply, and with the dorsal arm neither expanded apically nor with an acute projection. Fuscous spots are sometimes present on the vertex of *incerta*. Long-winged specimens have been examined. This species has been collected in Colorado, Kansas, Montana, Nebraska, New Mexico, and Wyoming, and appears to be a specialist on *Distichlis spicata*.

### *Athysanella kadokana* Knull
Figs. 62–65

*Athysanella kadokana* Knull 1951:180.

Length of male 2.7 to 3.4 mm, female 4.0 to 4.4 mm; head width of male 0.95 to 1.1 mm, female 1.1 to 1.25 mm; pronotal width of male 0.9 to 1.05 mm, female 1.05 to 1.15 mm; interocular width of male 0.4 to 0.5 mm, female 0.5 to 0.6 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.55 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.84 to 1.0 interocular width; pronotal length 0.72 to 0.82 vertex length.

Character code: 0-1-1-0-1-0-0-0-1-2-2-2-0-1-0-0-0-1.

Holotype, male, from Kadoka, South Dakota, Badlands, 19 July 1950 (H. C. Severin) at OhSU.

This species is closely related to *salsa* but can be separated by the shape of the male plate, which is rounded, and by the apex of the style, which has a more conspicuous ventral arm (Fig. 63). The shape of the posterior margin of the female sternum VII is variable in this species (Figs. 64, 65). Specimens parasitized with Pipinculidae and Dryinidae and specimens with undeveloped genitalia have been examined; occasionally a specimen with faint spots on the vertex is seen. This species, collected in Colorado, South Dakota, Montana, Nebraska, Wyoming, and Canada, appears to be a specialist on *Distichlis spicata*.

### *Athysanella salsa* Ball & Beamer
Figs. 66–70

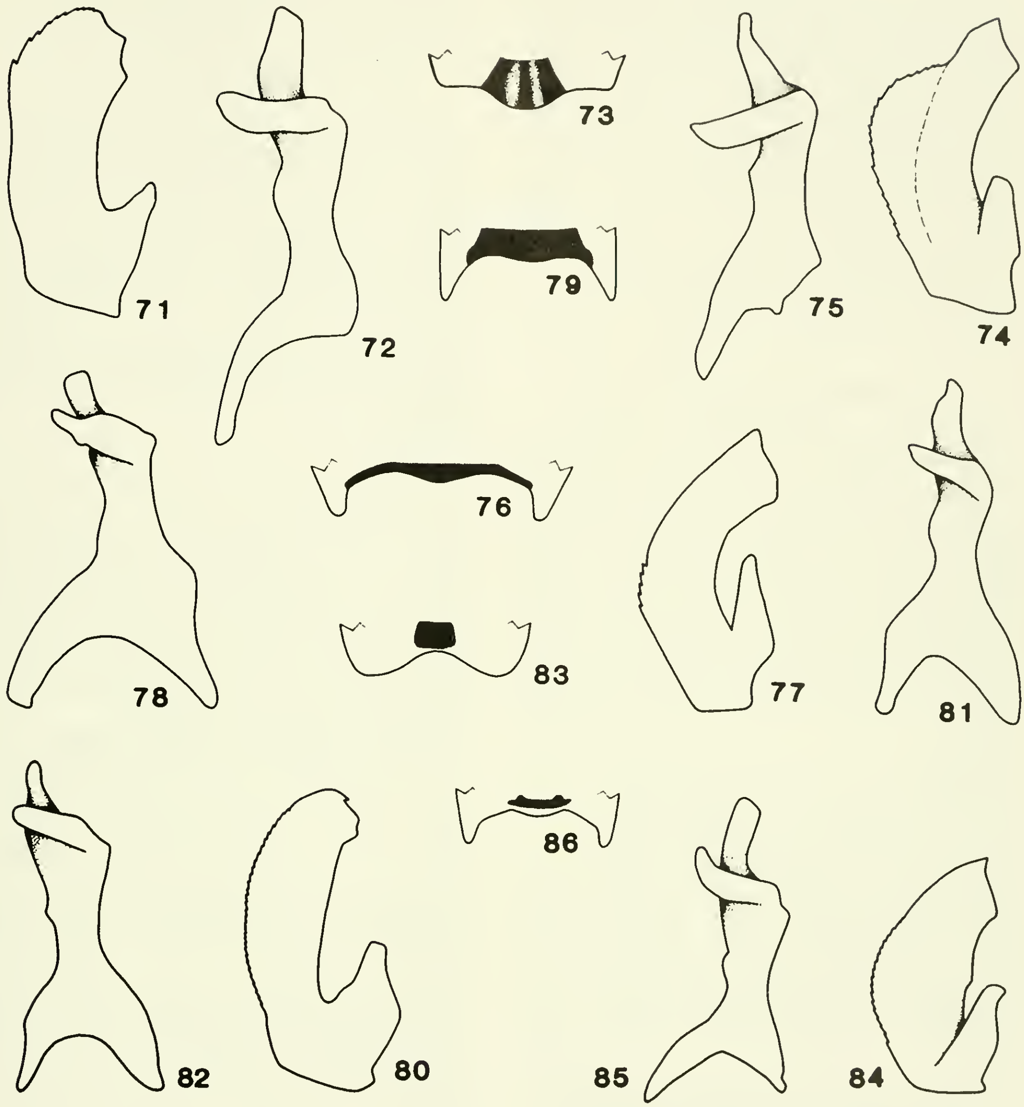
*Athysanella salsa* Ball & Beamer 1940:20.

Length of male 2.9 to 3.2 mm, female 3.6 to 4.4 mm; head width of male 1.0 to 1.15 mm, female 1.0 to 1.2 mm; pronotal width of male 0.9 to 1.05 mm, female 0.95 to 1.15 mm; interocular width of male 0.45 to 0.5 mm, female 0.45 to 0.55 mm; vertex length of male 0.4 to 0.5 mm, female 0.45 to 0.55 mm; pronotal length of male 0.3 to 0.4 mm, female 0.3 to 0.4 mm. Vertex length 0.94 to 1.1 interocular width; pronotal length 0.72 to 0.88 vertex length.

Character code: 0-1-1-0-2-0-0-0-2-1-2-2-0-1-0-0-0-0.

Holotype, male, and allotype, female, from St. John, Kansas, 11 Sept 1936 (R. H. Beamer) in KU.

*Athysanella salsa* is closely related to *kadokana* but can be separated by the truncate apices of the male plates and the less conspicuous ventral apical arm of the style (Fig. 68). Specimens studied from Mexico have fuscous spots on the vertex and dark stripes on the forewings. Long-winged females have been examined. Males and females parasitized by Dryinidae and undeveloped specimens have been examined. This species has been collected in Kansas, Texas, and Mexico, and appears to be a specialist on *Distichlis spicata*.




Figs. 71–86. Figs. 71–73. *Athysanella kanabana:* 71, aedeagus, lateral view; 72, style, broad aspect; 73, female sternum VII, ventral view. Figs. 74–76. *Athysanella furnaca:* 74, aedeagus, lateral aspect; 75, style, broad aspect; 76, female sternum VII, ventral view. Figs. 77–79. *Athysanella marthae:* 77, aedeagus, lateral view; 78, style, broad aspect; 79, female sternum VII, ventral view. Figs. 80–83. *Athysanella bifida:* 80, aedeagus, lateral view; 81, 82, style, broad aspect; 83, female sternum VII, ventral view. Figs. 84–86. *Athysanella utahna:* 84, aedeagus, lateral view; 85, style, broad aspect; 86, female sternum VII, ventral aspect.

### *Athysanella kanabana* Ball & Beamer
Figs. 71–73

*Athysanella kanabana* Ball & Beamer 1940:20.

Length of male 3.1 to 3.6 mm, female 4.4 to 4.7 mm; head width of male 1.1 to 1.2 mm, female 1.25 to 1.4 mm; pronotal width of male 1.05 to 1.15 mm, female 1.2 to 1.3 mm; interocular width of male 0.5 to 0.55 mm, female 0.6 to 0.7 mm; vertex length of male 0.4 to 0.5 mm, female 0.5 to 0.55 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.8 to 0.95 interocular width; pronotal length 0.76 to 0.88 vertex length.

Character code: 0-1-1-1-1-0-0-0-2-1-2-2-0-1-0-1-1-0.

Holotype, male, and allotype, female, from Kanab, Utah, 9 Aug 1936 (R. H. Beamer) in KU; paratypes in KU and USNM.

*Athysanella kanabana* is related to *tenera* but can be separated by the embrowned area on the plates, the aedeagus with apical crests on the shaft (Fig. 71), and the unique shape of the apex of the style (Fig. 72). Occasionally, there are fuscous spots on the vertex. Undeveloped specimens are represented in the paratype series. This species has been collected on *Sporobolus airoides* in Arizona, Kansas, New Mexico, and Utah.

*Athysanella furnaca* Blocker, n. sp.
Figs. 74–76

Length of male 3.1 mm, female 4.4 to 4.7 mm; head width of male 1.15 mm, female 1.25 to 1.3 mm; pronotal width of male 1.1 mm, female 1.2 to 1.25 mm; interocular width of male 0.5 mm, female 0.5 to 0.55 mm; vertex length of male 0.5 mm, female 0.5 to 0.55 mm; pronotal length of male 0.4 mm, female 0.4 to 0.45 mm. Vertex length equal to interocular width; pronotal length 0.78 to 0.79 vertex length.

Character code: 0-0-1-0-2-0-0-0-2-1-2-2-0-1-0-0-1-1.

Color stramineous, except for dark dots on abdomen and slight fuscous on legs.

Forewings brachypterous, exposing 3.5 pregenital abdominal terga; ocellus approximately 2X its diameter from eye; hind tibial spur 1/2 length (or less) of 1st tarsomere; female abdominal sternum VII (Fig. 76) with short lateral lobes and slight median projection.

Pygofer with caudal margin extended, exceeding anal tube, with approximately 25 setae; valve with caudal margin rounded; plates truncate apically, barely exceeding apex of valve; style with ventral arm short (Fig. 75), conspicuously flattened, dorsal arm elongate; connective 3/4 length of pygofer; aedeagus (Fig. 74) with conspicuous keels on shaft.

Holotype, male, from Death Valley, California, 5.7 mi N Furnace Cr., 19 March 1971 (Oman); two female paratypes, same data. Holotype and paratype in OrSU; paratype in KSU.

*Athysanella furnaca* is related to *kanabana* but can be distinguished by the medial crests on the shaft of the aedeagus and the connective, which is shorter than the style. This species is known only from the type locality in the Mojave Desert of California.

*Athysanella marthae* Blocker, n. sp.
Figs. 77–79

Length of male 2.9 to 3.3 mm, female 4.1 to 4.6 mm; head width of male 1.15 to 1.25 mm, female 1.25 to 1.35 mm; pronotal width of male 1.1 to 1.2 mm, female 1.1 to 1.2 mm; interocular width of male 0.45 to 0.5 mm, female 0.5 to 0.55 mm; vertex length of male 0.4 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.35 to 0.4 mm, female 0.4 to 0.45 mm. Vertex length 0.89 to 0.95 interocular width; pronotal length 0.82 to 0.94 vertex length.

Character code: 0-1-1-0-2-0-0-0-2-2-2-1-0-1-0-0-1-1.

Color uniformly stramineous, except for irregular, fuscous markings on venter and legs.

Forewings brachypterous, exposing 3 to 4.5 pregenital abdominal terga; ocellus approximately 2X its diameter from eye; hind tibial spur 2/3 length of 1st tarsomere; female abdominal sternum VII (Fig. 79) with conspicuous lateral lobes on hind margin.

Pygofer broadly rounded apically, with fewer than 25 macrosetae, exceeding apex of plates; anal tube exceeding the apex of pygofer; valve with caudal margin rounded; plates short, truncate, with conspicuous microsetae; style (Fig. 78) with conspicuous lateral flange and preapical lobe, deeply bifid apically, dorsal arm truncate, ventral arm rounded, exceeding apex of plates and pygofer; connective 3/4 length of style; aedeagus (Fig. 77) with caudal margin of shaft serrate, troughlike in caudal view, with inconspicuous process apically, dorsal apodeme simple.

Holotype, male, from Cuatro Cienegas, Coahuila, Mexico, 9 June 1985, (A. L. Hicks) 1266B; five male and five females paratypes, same data. Holotype and paratypes in KSU; paratypes in IPL.

*Athysanella marthae* is related to *bifida* but can be distinguished by the conspicuous lateral flange of the style and the short, truncate plates. This species has been collected only at the type locality in Mexico on *Monanthochloe littoralis*. I name this species for my wife.

*Athysanella bifida* Ball & Beamer
Figs. 80–83

*Athysanella bifida* Ball & Beamer 1940:23.

Length of male 2.4 to 3.0 mm, female 3.1 to 3.7 mm; head width of male 0.9 to 1.05 mm, female 0.95 to 1.1 mm; pronotal width of male 0.8 to 1.0 mm, female 0.9 to 1.0 mm; interocular width of male 0.4 to 0.45 mm, female 0.4 to 0.5 mm; vertex length of male 0.35 to 0.45 mm, female 0.4 to 0.5 mm; pronotal length of male 0.25 to 0.35 mm, female 0.3 to 0.35 mm. Vertex length 0.87 to 1.0 interocular width; pronotal length 0.7 to 0.82 vertex length.

Character code: 0-1-1-0-1-0-0-0-1-2-2-1-0-1-0-0-1-0.

Holotype, male, and allotype, female, from Monument, Colorado, 19 Aug 1936 (R. H. Beamer) in KU; paratypes in KU and USNM.

*Athysanella bifida* is related to *utahna* and *yumana* but can be separated by the elongate shaft of the aedeagus (Fig. 80), which is not widened at midlength. Specimens parasitized by Dryinidae and Strepsiptera, undeveloped specimens, and long-winged specimens have been examined. This species has been collected in Arizona, Colorado, Montana, New Mexico, North Dakota, South Dakota, Texas, Wyoming, and Canada. In the southern part of its range, at least, the host is blue grama, *Bouteloua gracilis* (Hicks et al. 1988).

### *Athysanella utahna* Osborn
Figs. 84–86

*Athysanella utahna* Osborn 1930:705.

Length of male 2.6 to 3.3 mm, female 3.9 to 4.9 mm; head width of male 0.9 to 1.05 mm, female 1.05 to 1.25 mm; pronotal width of male 0.85 to 1.0 mm, female 1.0 to 1.1 mm; interocular width of male 0.35 to 0.45 mm, female 0.45 to 0.55 mm; vertex length of male 0.4 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.3 to 0.4 mm. Vertex length 0.94 to 1.13 interocular width; pronotal length 0.7 to 0.82 vertex length.

Character code: 0-1-0-0-1-0-0-0-2-1-2-0-0-1-0-0-1-1.

Lectotype, male, and lectoallotype, female, from Ephraim, Utah, 20 July 1914 (E. D. Ball) in USNM.

*Athysanella utahna* is related to *yumana* but can be separated by the more slender apical dorsal arm and less robust ventral arm of the style (Fig. 85). It can be separated from *bifida* by the shorter shaft of the aedeagus (Fig. 84). Rarely a specimen is seen with fuscous spots on the vertex; the styles occasionally have a macroseta. Specimens with long wings and undeveloped genitalia and specimens parasitized by Dryinidae and Pipinculidae have been examined. This species has been collected in Arizona, California, Colorado, Idaho, Nevada, Utah, Oregon, Washington, Canada, and Mexico. Reported from saltgrass, *Distichlis spicata*, in Mexico and Utah.

### *Athysanella yumana* Osborn
Figs. 87–89

*Athysanella yumana* Osborn 1930:704.

Length of male 2.8 to 3.1 mm, female 3.8 to 4.7 mm; head width of male 1.05 to 1.15 mm, female 1.1 to 1.25 mm; pronotal width of male 0.95 to 1.1 mm, female 1.0 to 1.2 mm; interocular width of male 0.4 to 0.45 mm, female 0.45 to 0.55 mm; vertex length of male 0.4 to 0.45 mm, female 0.45 to 0.50 mm; pronotal length of male 0.3 to 0.35 mm, female 0.3 to 0.4 mm. Vertex length 0.94 to 1.0 interocular width; pronotal length 0.76 to 0.82 vertex length.

Character code: 1-1-1-0-2-0-0-0-2-1-2-2-0-1-0-0-1-0.

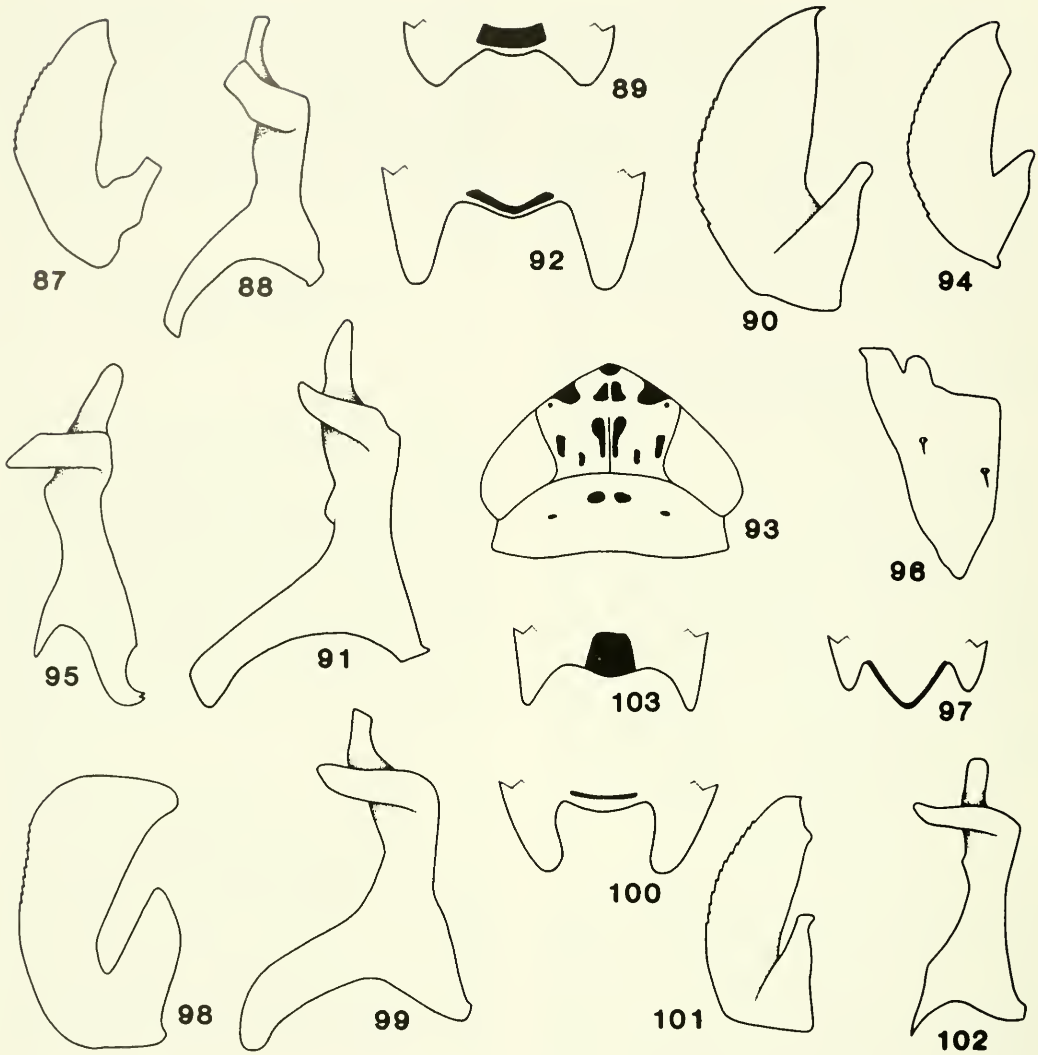
Lectotype, male, and lectoallotype, female, from Yuma, Arizona (H. Osborn) in USNM; paratypes in USNM and KU.

*Athysanella yumana* is related to *utahna* but can be separated by the shape of the apex of the style (Fig. 88), which has more robust ventral and dorsal arms. Occasionally, there are fuscous spots on the vertex. The style may have an occasional macroseta. This species has been reported from saltgrass, *Distichlis spicata;* it has been collected in Arizona and California.

### *Athysanella deserta* Blocker, n. sp.
Figs. 90–92

Length of male 3.0 to 3.3 mm, female 4.3 to 4.8 mm; head width of male 1.1 to 1.2 mm, female 1.2 to 1.3 mm; pronotal width of male 1.05 to 1.15 mm, female 1.15 to 1.25 mm; interocular width of male 0.45 to 0.5 mm, female 0.5 to 0.6 mm; head width of male 0.45 to 0.5 mm, female 0.5 to 0.6 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.9 to 1.0 interocular width; pronotal length 0.75 to 0.83 vertex length.

Character code: 0-0-1-0-2-0-1-0-2-2-2-2-0-1-0-0-1-1.




Figs. 87–103. Figs. 87–89. *Athysanella yumana:* 87, aedeagus, lateral view; 88, style, broad aspect; 89, female sternum VII, ventral view. Figs. 90–92. *Athysanella deserta:* 90, aedeagus, lateral view; 91, style, broad aspect; 92, female sternum VII, ventral view. Figs. 93–97. *Athysanella magdalena:* 93, head and pronotum, dorsal view; 94, aedeagus, lateral view; 95, style, broad aspect; 96, male plate, ventral view; 97, female sternum VII, ventral view. Figs. 98–100. *Athysanella laeta:* 98, aedeagus, lateral view; 99, style, broad aspect; 100, female sternum VII, ventral view. Figs. 101–103. *Athysanella stylosa:* 101, aedeagus, lateral view; 102, style, broad aspect; 103, female sternum VII, ventral view.

Color stramineous; faint orange pattern often seen on vertex; faint fuscous dots may be present on abdominal terga; face usually with faint lateral lines; venter with various amounts of fuscous coloring.

Forewings brachypterous, exposing 3.5 to 4.0 pregenital abdominal terga; ocellus approximately 1.5 its diameter from eye; hind tibial spur 1/3 to 1/2 length of 1st tarsomere; female abdominal sternum VII (Fig. 92) with conspicuous lateral lobes, inconspicuous medial lobe rounded, with various amounts of fuscous coloring.

Pygofer with caudal margin rounded, with 25+ microsetae; plates separated at base, truncate apically, not reaching apex of pygofer; anal tube exceeding apex of pygofer; valve with caudal margin rounded; connective 2/3 length of style; styles (Fig. 91) slightly exceeding apex of pygofer with apical arm

enlarged at apex, ventral arm with small, acute process; aedeagus (Fig. 90) with shaft narrowed apically, finely serrate on ventral margin, approximately 2X length of dorsal apodeme.

Holotype, male, from Death Valley, California, 36 mi S Furnace Cr., 19 March 1971 (Oman); 18 male and 15 female paratypes, same data. Holotypes and paratypes in OrSU; paratypes in KSU.

*Athysanella deserta* is related to *yumana* but can be separated by the shape of the apical arms of the style with the dorsal arm enlarged at the apex and the ventral arm with a small, acute process. This species has been collected only at the type locality in the Mojave Desert of California.

### *Athysanella magdalena* Baker
Figs. 93–97

*Athysanella magdalena* Baker 1898:185.

Length of male 2.2 to 2.7 mm, female 3.0 to 3.6 mm; head width of male 0.85 to 0.95 mm, female 0.95 to 1.1 mm; pronotal width of male 0.75 to 0.9 mm, female 0.9 to 1.1 mm; interocular width of male 0.3 to 0.4 mm, female 0.4 to 0.5 mm; vertex length of male 0.3 to 0.4 mm, female 0.35 to 0.45 mm; pronotal length of male 0.25 to 0.35 mm, female 0.3 to 0.35 mm. Vertex length 0.93 to 1.1 interocular width; pronotal length 0.8 to 0.91 vertex length.

Character code: 1-1-0-0-0-0-0-0-2-0-1-0-1-0-0-1-0.

Lectotype, female, from Magdalena Mts., New Mexico, Aug 1894 (F. H. Snow), and lectoallotype, male, from Forrester's Ranch, Laramie Co., Colorado, 3 Aug 1896 (No. 2013 of Baker) in USNM.

*Athysanella magdalena* is related to *tenera* but can be separated by the elongate plates and the shape of the apex of the style (Fig. 95), which is more clearly bifid. Plates occasionally have one or more macrosetae, and occasionally the male hind tibial spur is undeveloped. Numerous undeveloped specimens, specimens parasitized by Dryinidae and Strepsiptera, and long-winged males and females have been examined. This species, collected in Arizona, California, Colorado, Montana, New Mexico, Nevada, Oklahoma, Texas, Utah, Wyoming, and Mexico, is a common specialist of blue grama, *Bouteloua gracilis* (Whitcomb et al. 1987, Hicks et al. 1988).

### *Athysanella laeta* Ball & Beamer
Figs. 98–100

*Athysanella laeta* Ball and Beamer, 1940:16.

Length of male 2.7 to 2.9 mm, female 3.8 to 4.1 mm; head width of male 1.0 to 1.1 mm, female 1.1 to 1.2 mm; pronotal width of male 0.95 to 1.05 mm, female 1.05 to 1.15 mm; interocular width of male 0.45 to 0.5 mm, female 0.5 to 0.55 mm; vertex length of male 0.35 to 0.4 mm, female 0.4 to 0.45 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.75 to 0.89 interocular width; pronotal length 0.87 to 1.0 vertex length.

Character code: 1-1-1-0-2-0-0-0-2-1-2-0-0-1-0-0-1-1.

Holotype, male, from Huachuca Mts., Arizona, 15 July 1934 (E. D. Ball); allotype, female, same data except 14 July, in USNM; paratypes in USNM and KU.

*Athysanella laeta* is related to *incongrua* but can be separated by its usually smaller size and the shape of the shaft of the aedeagus (Fig. 98), which is shorter and not as avicephaliform apically. Some of the male paratypes have undeveloped genitalia. This species has been collected in New Mexico and Arizona.

### *Athysanella stylosa* Blocker, n. sp.
Figs. 101–103

Length of male 2.4 to 2.8 mm, female 3.8 to 4.1 mm; head width of male 0.95 to 1.1 mm, female 1.15 to 1.2 mm; pronotal width of male 0.9 to 1.0 mm, female 1.05 to 1.1 mm; interocular width of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; vertex length of male 0.35 to 0.45 mm, female 0.4 to 0.5 mm; pronotal length of male 0.3 to 0.35 mm, female 0.3 to 0.4 mm. Vertex length 0.93 to 1.06 interocular width; pronotal length 0.75 to 0.82 vertex length.

Color stramineous with brown pattern on vertex and pronotum, vertex with fuscous spots, wings with brown stripes, face with brown arcs.

Forewings brachypterous, exposing 3 to 4.5 pregenital abdominal terga; ocellus approximately its diameter from eye; hind tibial spur 3/4 1st tarsomere; female abdominal sternum VII (Fig. 103) with well-developed lateral lobes, slightly concave medially.

Pygofer broadly rounded apically, with fewer than 25 setae; anal tube exceeds apex of

pygofer; valve with caudal margin rounded; plates rounded apically; styles (Fig. 102) bifid, dorsal arm acute, ventral arm truncate, without lateral flange or preapical lobe, exceeding apex of plates and pygofer; connective 3/4 length of style; aedeagus (Fig. 101) with shaft serrate on caudal margin, troughlike in caudal view, with inconspicuous process apically.

Holotype, male, from Roswell, Chaves Co., New Mexico, Bitter Lake Natl. WLR, 14 Aug 1984 (R. F. Whitcomb) 0868A; 17 male and 7 female paratypes, same data; 1 male paratype, same data except 21 Aug 1985, 01931. Holotype and paratypes in KSU; paratypes in USNM and IPL.

*Athysanella stylosa* is related to *supina* but can be distinguished by the fuscous spots on the vertex and by the shaft of the aedeagus, which is not as widened medially. This species is different in that the vertex length is equal to the interocular width and fuscous spots are present. It has been collected on gyp dropseed, *Sporobolus nealleyi*, in the gypsum flats of southeastern New Mexico.

### *Athysanella incongrua* Baker
Figs. 104–106

*Athysanella incongrua* Baker 1898:188.

Length of male 3.0 to 3.4 mm, female 4.2 to 4.8 mm; head width of male 1.1 to 1.2 mm, female 1.15 to 1.35 mm; pronotal width of male 1.05 to 1.15 mm, female 1.1 to 1.25 mm, interocular width of male 0.45 to 0.5 mm, female 0.55 to 0.65 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.76 to 0.85 interocular width; pronotal length 0.88 to 1.0 vertex length.

Character code: 1-1-0-0-2-1-0-0-2-1-2-2-0-1-0-0-0-0.

Lectotype, male, from Fort Collins, Colorado, 21 July (C. F. Baker) in USNM.

*Athysanella incongrua* is related to *laeta* and *terebrans* but can be separated by the length and shape of the apex of the shaft of the aedeagus (Fig. 104). The fuscous spots on the vertex are commonly missing. Long-winged males and females have been examined. Specimens, collected in Colorado, Iowa, Kansas, Nebraska, New Hampshire, New Mexico, Oklahoma, South Dakota, Texas, and Wyoming, appear to be associated with little bluestem, *Schizachyrium scroparium*. The specimen from New Hampshire was collected by P. W. Oman at Wiley House, 20 Aug 1934.

### *Athysanella tenera* Ball & Beamer
Figs. 107–109

*Athysanella tenera* Ball & Beamer 1940:17.

Length of male 2.5 to 3.0 mm, female 3.9 to 4.0 mm; head width of male 1.0 to 1.1 mm, female 1.1 to 1.2 mm; pronotal width of male 0.9 to 1.0 mm, female 1.0 to 1.15 mm; interocular width of male 0.4 to 0.45 mm, female 0.45 to 0.5 mm; vertex length of male 0.35 to 0.45 mm, female 0.4 to 0.45 mm; pronotal length of male 0.3 to 0.35 mm, female 0.35 to 0.4 mm. Vertex length 0.94 to 1.0 interocular width; pronotal length 0.76 to 0.8 vertex length.

Character code: 1-1-0-0-1-0-0-0-1-0-2-2-0-1-0-0-1-0.

Holotype, male, and allotype, female, from Las Vegas, Nevada, 8 Aug 1936 (R. H. Beamer) in KU; paratypes in KU.

*Athysanella tenera* is related to *magdalena* but can be distinguished by the shorter plates and the irregular shape of the outer apical arm of the style (Fig. 108), which is widened and appears to be trifid. This species is known only from the type locality in Nevada.

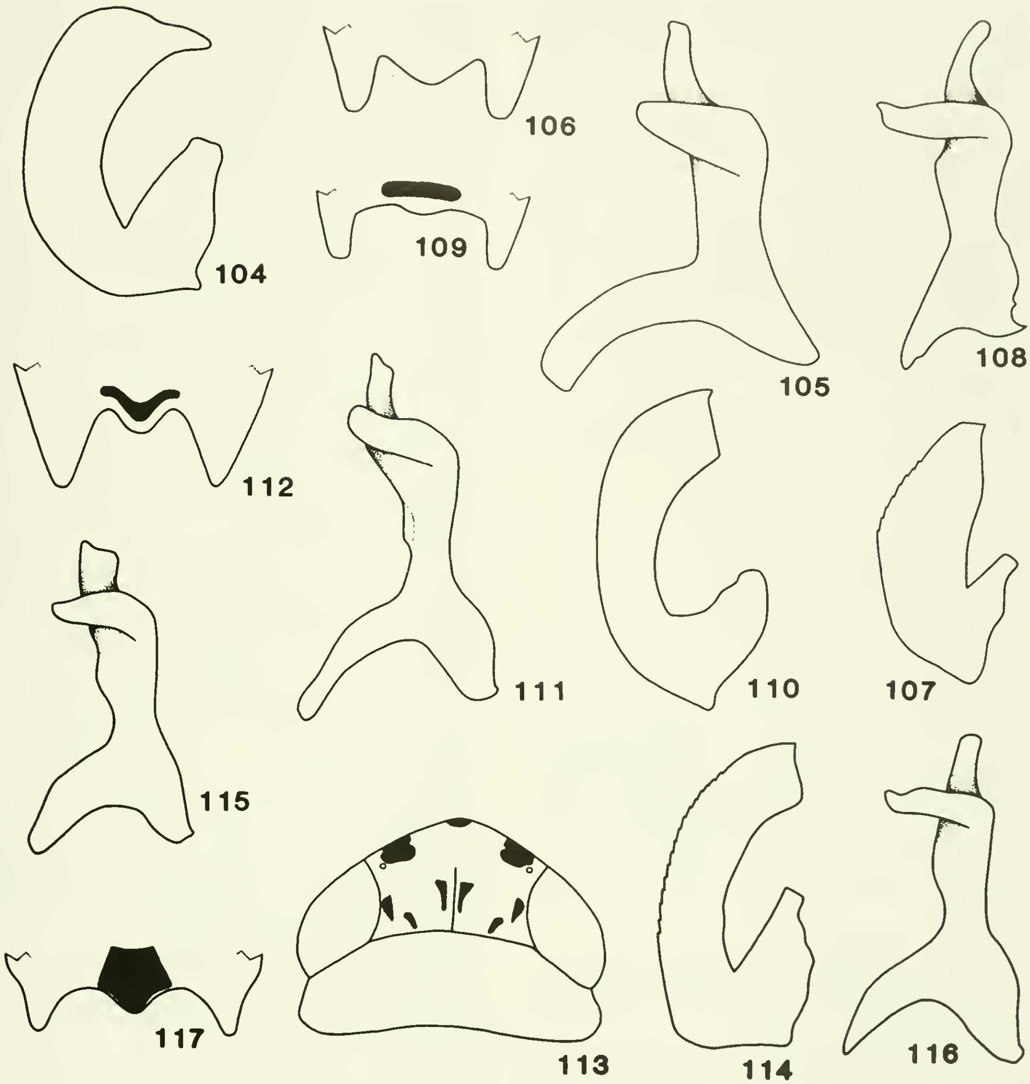
### *Athysanella vativala* Blocker, n. sp.
Figs. 110–112

Length of male 2.9 to 3.2 mm, female 4.2 to 4.6 mm; head width of male 1.05 to 1.15 mm, female 1.25 to 1.35 mm; pronotal width of male 1.0 to 1.15 mm, female 1.15 to 1.3 mm; interocular width of male 0.4 to 0.55 mm, female 0.55 to 0.65 mm; vertex length of male 0.35 to 0.5 mm, female 0.45 to 0.55 mm; pronotal length of male 0.35 to 0.4 mm, female 0.35 to 0.45 mm. Vertex length 0.78 to 0.9 interocular width; pronotal length 0.74 to 0.94 vertex length.

Character code: 1-0-0-0-1-0-0-0-1-1-1-0-0-1-0-0-1-0.

Color stramineous; vertex with fuscous spots; vertex, pronotum, and abdomen with additional brown pattern; forewings with darkened stripes; face with lateral fuscous marks; legs with fuscous areas.

Forewings brachypterous, exposing 4 to 4.5 pregenital abdominal terga; ocellus 2X its diameter from eye or less; hind tibial spur 1/2 length of 1st tarsomere; female abdominal




Figs. 104–117. Figs. 104–106. *Athysanella incongrua:* 104, aedeagus, lateral view; 105, style, broad aspect; 106, female sternum VII, ventral view. Figs. 107–109. *Athysanella tenera:* 107, aedeagus, lateral view; 108, style, broad aspect; 109, female sternum VII, ventral view. Figs. 110–112. *Athysanella vativala:* 110, aedeagus, lateral view; 111, style, broad aspect; 112, female sternum VII, ventral view. Figs. 113–117. *Athysanella terebrans:* 113, head and pronotum, dorsal view; 114, aedeagus, lateral view; 115, 116, style, broad aspect; 117, female sternum VII, ventral view.

sternum VII (Fig. 112) with lateral lobes much longer than medial lobe.

Pygofer rounded apically, fewer than 25 macrosetae; valve with caudal margin angulate; plates separated at base, rounded apically; connective 3/4 length of style; styles (Fig. 111) deeply bifid, dorsal arm elongate and slender, ventral arm thickened, no preapical lobe present; aedeagus, in lateral view, with shaft slightly widened in apical half (Fig. 110), troughlike on ventral margin, and slightly serrate.

Holotype, male, from Sheridan Co., Nebraska, 7 mi N Rushville, Hwy 87, 9 Aug 1979 (H. D. Blocker and R. A. Sweet); female paratype, same data; 4 male and 7 female paratypes, Cherry Co., Nebraska, S Valentine, Hwy 83, mi 202, 10 Aug 1979 (H. D. Blocker and R. A. Sweet); 2 males, Cherry Co., Nebraska, near Manker, Hwy 20, 9 Aug 1979 (H. D. Blocker and R. A. Sweet); 1 male, Bowman, North Dakota, 5 July 1968, GL 819 (Harris and Cooley); 2 males and 10 females, Tryon, McPherson Co., Nebraska, 7 Aug

1977, (R. F. Whitcomb) 0480. Holotype and paratypes in KSU; paratypes in CNC, IPL, USNM.

*Athysanella vativala* is very closely related and possibly conspecific with *terebrans* but can be separated by the shape of the apex of the style, which has a more slender dorsal arm, a more patterned and longer vertex, and the ocelli usually more distant from the eye. Undeveloped specimens and specimens parasitized with Strepsiptera have been examined. This species has been collected in Nebraska and North Dakota on *Calanovilfa longifolia*.

*Athysanella terebrans* (Gillette & Baker)
Figs. 113–117

*Euttetix terebrans* Gillette & Baker 1895:102.

Length of male 2.7 to 3.1 mm, female 4.2 to 4.6 mm; head width of male 1.0 to 1.15 mm, female 1.2 to 1.35 mm; pronotal width of male 0.95 to 1.05 mm, female 1.15 to 1.3 mm; interocular width of male 0.45 to 0.5 mm, female 0.55 to 0.6 mm; vertex length of male 0.35 to 0.45 mm, female 0.45 to 0.5 mm; pronotal length of male 0.3 to 0.4 mm, female 0.4 to 0.45 mm. Vertex length 0.75 to 0.89 interocular width; pronotal length 0.82 to 1.0 vertex length.

Character code: 1-0-0-0-1-0-0-0-1-1-1-0-0-1-0-0-1-0.

Holotype, female, from North Park, Colorado, 30 July (Gillette) in USNM; allotype, male, from Wray, Colorado, 13 July 1899, at Colorado State University.

*Athysanella terebrans* is related to *incongrua* but can be distinguished by the dorsal apical arm of the style (Figs. 115, 116), which is rounded, and by the shaft of the aedeagus (Fig. 114), which is not conspicuously widened apically; the female abdominal sternum VII (Fig. 117) may be variable in shape. Long-winged and undeveloped specimens were commonly examined. This species has been collected in Colorado, Montana, Nebraska, North Dakota, South Dakota, Utah, Wyoming, and Canada. It is reported from *Dystichlis stricta* in Manitoba.

## PHYLOGENY

Phylogeny of the subgenera of *Athysanella* is discussed in Blocker and Johnson (1988). The subgenus *Athysanella* is designated a sister of *Gladionura* and can be separated by the absence of a pygofer process in the former. The presence of a pygofer process is a convergent character that occurs in two other less closely related subgenera. We selected 40 characters that show differences within the subgenus for analysis. An intuitive phylogeny based on the proposed sequence of occurrence of major derived characters was generated, as well as an analysis by PAUP (Swofford 1986). Results of these analyses are shown in Figures 118 and 119. PAUP generated five equally most parsimonious trees; the tree with no unresolved trifurcations is presented here. A hypothetical ancestor consisting of a uniform plesiomorphic character set was utilized. Character sequences are contained in the preceding descriptions; the entire PAUP data set is available on request. Overall, the PAUP cladogram and the intuitive phylogeny are in good agreement. Species groups 1, 3, 4, and 7 are consistently grouped together (Fig. 119), whereas the *rostrata* and *incongrua-planata* groups are widely fragmented. It is possible that this fragmentation of the groups is indicative of the high degree of homoplasy in the genus.

The *robusta* group is characterized by retention of the rounded shape of the style apex; the male plates are embrowned in all species (2′); the styles are widened and often bifid apically in all other species (1′). This group is recognized in the PAUP output.

The *rostrata* group has an extended apex of the male style (1″); PAUP has the species in this group occurring close together but none as sisters.

The *incerta* group is characterized by the presence of a semicircular apex of the shaft of the aedeagus (3′). There is fairly good congruence in the cladogram, which includes *planata* as a sister of *incerta*.

The *terebrans-bifida* group is characterized by an aedeagal shaft that is serrate on the caudal margin (4′). The *terebrans* group has a shortened vertex (5′); five of the seven species are recognized by PAUP; the other two (*laeta* and *marthae*) split out sooner but are close. The *bifida* group retains an elongate vertex; they are represented in the last half of the cladogram, close together, but only *bifida* and *magdalena* are sisters.

The *incongrua-planata* group retains an aedeagus with a simple shaft. PAUP separates

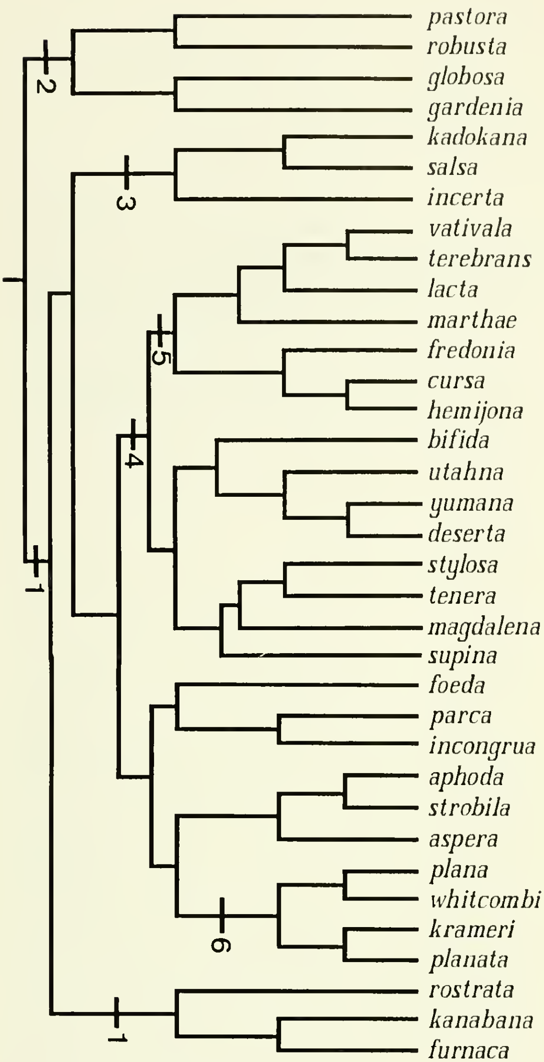



Fig. 118. Intuitive cladogram.

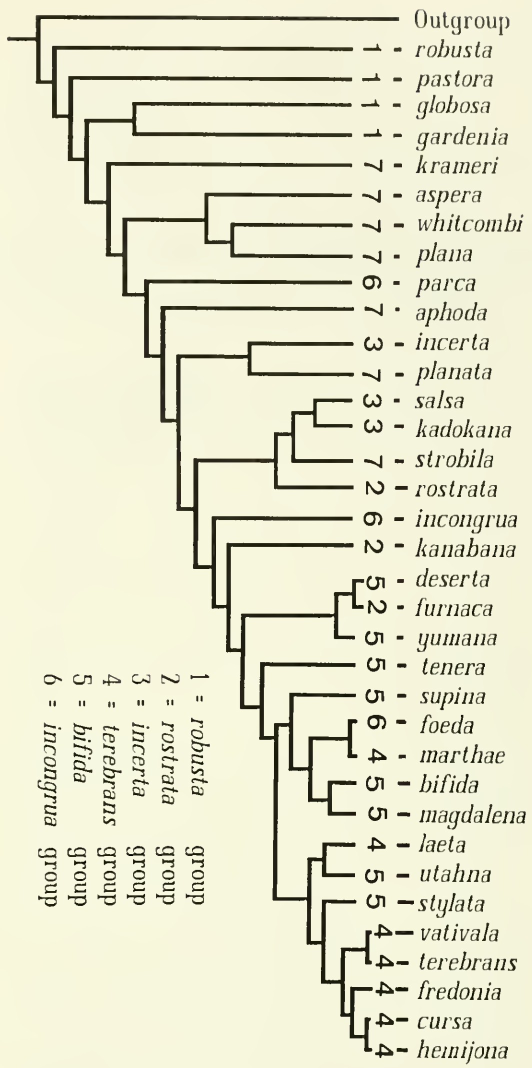



Fig. 119. PAUP cladogram.

the *incongrua* group to a greater degree than any other group in the intuitive cladogram. The *planata* group species are characterized by an ocellus that is more remote from the eye than other groups (6′) and all split out in the first half of the PAUP cladogram. Four species (*krameri*, *aspera*, *whitcombi*, and *plana*) arise from the cladogram in sequence.

ACKNOWLEDGMENTS

Paul Oman has always been gracious and very helpful in his support of leafhopper systematics; it is a high honor to contribute to a volume dedicated to his many contributions to our science. Merv Nielson collected with the senior author in Mexico and elsewhere and has offered assistance throughout this study. Likewise, the assistance of Bob Whitcomb and Andy Hicks has added significantly, particularly with host information and species distribution. Bob Brooks frequently furnished work space in the Snow Entomological Museum. Paul Cwikla has read drafts of this and related manuscripts, and Jeffry Ediger, a student at KSU, inked the illustrations of the genitalia.

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# A NEW GENUS, *ILEOPELTUS*, RELATED TO *CHLOROTETTIX* (HOMOPTERA: CICADELLIDAE)

Paul S. Cwikla[1]

ABSTRACT.—On the basis of their unique genitalic characters, the Neotropical leafhopper species previously treated in the genus *Doleranus* Ball are placed in a new genus, *Ileopeltus*. Twelve species are treated, including six described as new. A key to the species and a cladistic hypothesis using *Chlorotettix* Van Duzee as the outgroup are presented. The new species of *Ileopeltus* include: *nanocanthus* (Panama), *dorsalus* and *clavatus* (Brazil and Venezuela), *ventriculus* and *haplus* (Brazil), and *blockeri* (Venezuela).

This paper is the first in a series of revisions dealing with the New World deltocephaline genera, which have their crown completely microsculptured. These leafhoppers, commonly called the broad-headed leafhoppers, are best known from the genus *Chlorotettix* Van Duzee. Species of this genus are commonly found in low-lying, grassy habitats of North and South America.

Traditionally, those leafhoppers with a completely microsculptured crown have been restricted to two genera, *Chlorotettix* Van Duzee and *Doleranus* Ball (Oman 1949). Linnavuori (1959) mentioned that some species of *Paratanus* Young and *Stirellus* Osborn & Ball also have their crown microsculptured, although no degree of phylogenetic relationship was implied.

More recently, I (Cwikla 1988) examined the North American species of *Doleranus* and found that they fell within an acceptable range of variation for *Chlorotettix*. I did not, however, consider the Neotropical species of *Doleranus* congeneric with *Chlorotettix* because of the following synapomorphies: the asymmetrical aedeagus, the aedeagus without processes, and, with the exception of only two species, the male plates fused with the valve. Because of these unique attributes, the Neotropical species of *Doleranus* treated by Linnavuori (1959) and six species described as new are designated a new genus, *Ileopeltus*.

Virtually nothing is known about the biology of *Ileopeltus* species. *Ileopeltus tethys* has been collected from sugar cane, weeds, sweet potato (Wolcott 1923), and grassy pastures (Caldwell and Martorell 1950) in Puerto Rico. Hosts for the other species of *Ileopeltus* are probably grasses.

With the exception of *I. tethys*, specimens of *Ileopeltus* species are rare in collections. For the most part they appear restricted between the Tropic of Cancer and the Tropic of Capricorn. Specimens have been collected in low- to mid-altitude areas.

Twelve species are included in this new genus, of which six are described as new. In addition, this paper provides a key to the species and a discussion of the phylogenetic relationships among the species. Specimens were prepared for SEM study as described in Cwikla and Freytag (1983). Names of institutions associated with abbreviations used in the text are in the acknowledgments section.

## *Ileopeltus*, n. gen.

DIAGNOSIS.—*Ileopeltus* species can be separated from other deltocephaline genera by the asymmetrical aedeagus without processes and the crown completely microsculptured.

COLOR.—Yellowish green or ochraceous. Markings occasionally present on crown and forewing.

STRUCTURAL FEATURES.—Small, deltocephaline leafhoppers. Crown roundly produced, median length slightly longer than length next to eye. Clypellus not constructed proximally. Forewing with cross-vein in claval area.

MALE GENITALIA.—Pygofer roundly produced or truncated, process present or absent. Anal tube weakly sclerotized dorsally. Valve acutely triangular, usually fused to plate posteriorly. Plate short or slightly longer than

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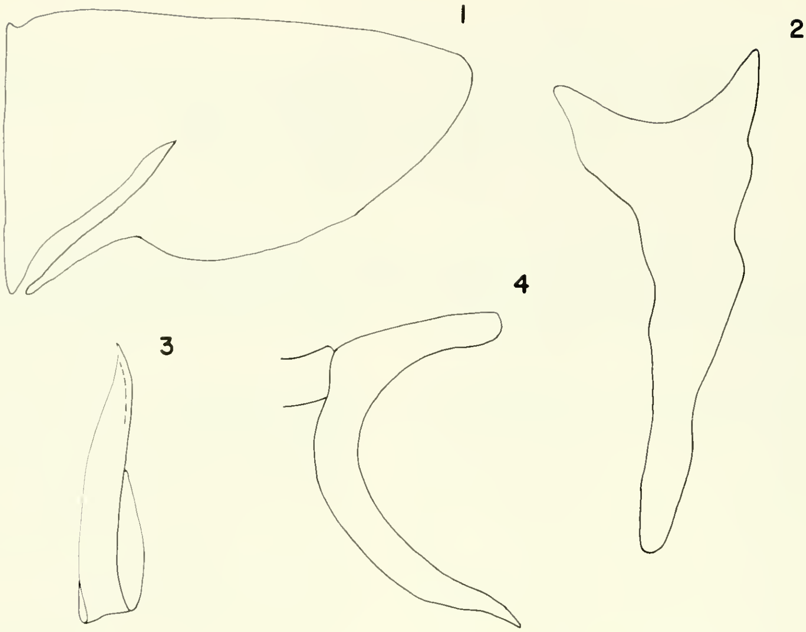



Figs. 1–4. *Ileopeltus tethys* Van Duzee: 1, pygofer, left lateral aspect; 2, right style, dorsal aspect; 3, aedeagus, ventral aspect; 4, aedeagus and apex of connective, left lateral aspect.

pygofer, rounded apically, macrosetae uniseriate, second short row of microsetaelike structures occasionally present, lateral margin sinuate, straight, or slightly convex. Stylar apex linear, preapical angle usually absent. Connective as long as or shorter than aedeagus. Aedeagus without processes, asymmetrical, apex acute in posterior aspect. Gonopore on right side at base of shaft.

TYPE SPECIES.—*Chlorotettix tethys* Van Duzee 1907:71.

DISTRIBUTION.—Neotropical, usually restricted between the Tropic of Cancer and the Tropic of Capricorn.

NOTES.—This genus has been previously described as *Doleranus* by Linnavuori (1959). The Neotropical species are not considered congeneric with the Nearctic forms and have been treated as synonyms of *Chlorotettix* (including the type species of *Doleranus*, *Thamnotettix longulus* Gillette & Baker) in a dissertation by Cwikla (1988).

Key to the Male *Ileopeltus* Species

1. Pygofer without a process (Fig. 1), or if present then extremely small (Fig. 7) ....... 2

— Pygofer with long, distinct processes (Fig. 43) 3

2(1). Pygofer without a process (Fig. 1) ......... ........................ *tethys* (Van Duzee)

— Pygofer with short process on posterodorsal margin in lateral aspect ....... *nanocanthus*, n. sp.

3(1). Stylar apex curved laterally (Fig. 52) ....... ........................ *cyclops* (Linnavuori)

— Stylar apex linear (Figs. 12, 30) ............ 4

4(3). Pygofer with process directed ventrad in lateral aspect ............... *ventriculus*, n. sp.

— Pygofer with process directed mesad or dorsad in lateral aspect ...................... 5

5(4). Pygofer with process heavily sclerotized, inserted on medial side in lateral aspect (Fig. 27) .................................. 8

— Pygofer with process not heavily sclerotized, not inserted on medial side in lateral aspect (Fig. 11) ............................. 6

6(5). Aedeagal shaft wide in ventral aspect (Fig. 25) ............................ *haplus*, n. sp.

— Aedeagal shaft narrow in ventral aspect (Fig. 22) .................................. 7

7(6). Stylar apex truncate (Fig. 12) .. *dorsalus*, n. sp.

— Stylar apex narrow (Fig. 20) . *spinosus* (DeLong)

8(5). Stylar apex truncate and constricted subapically (Fig. 40) ................ *clavatus*, n. sp.

— Stylar apex rounded or if truncate, then not constricted subapically ................... 9

9(8). Pygofer with process inserted on middle of ventral margin (Fig. 33) ....... *blockeri*, n. sp.

— Pygofer with process inserted on posteroventral margin (Figs. 27, 49) ................ 10

10(9). Aedeagus wide and highly asymmetrical in

5

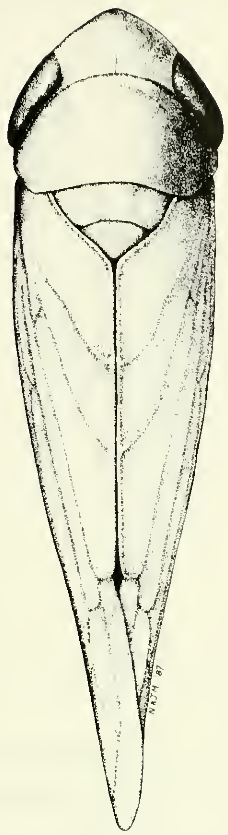


Fig. 5. *Ileopeltus tethys* Van Duzee, dorsal habitus.

ventral aspect (Fig. 49) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *cuneus* (DeLong & Martinson)

— Aedeagus narrow in ventral aspect . . . . . . . . 11

11(10). Aedeagus with large gonopore in lateral aspect (Fig. 32); plate fused with valve . . . . . . . . . . . . . . . . . . . . *hastulus* (DeLong & Linnavuori)

— Aedeagus with small gonopore in lateral aspect (Fig. 46); plate not appearing fused with valve . . . . . . . . . . . . . . . . . . . . *aberrans* (Osborn)

## *Ileopeltus tethys* (Van Duzee), n. comb.

Figs. 1–5, 57, 59; Map 1

*Chlorotettix tethys* Van Duzee 1907:71.
*Chlorotettix bidentatus* DeLong 1923:264, Wolcott 1936: 86.
*Chlorotettix dilutus* Osborn 1923:73, Osborn 1935:118.
*Doleranus kinonanus* Ball 1936:432, Linnavuori 1959: 274–275.

DIAGNOSIS.—*Ileopeltus tethys* is near *I. nanocantus* and can be separated from it and other *Ileopeltus* species by the lack of a pygoferal spine.

LENGTH.—Male 3.8–4.8 mm, female 4.1–5.4 mm.

COLOR.—Yellowish green. Eye reddish brown. Forewing yellowish subhyaline, small brown patch occasionally present on middle of wing and/or on claval area.

MALE GENITALIA.—Pygofer with posterior margin roundly produced, processes absent. Plate short, approximately half the length of pygofer, lateral margin straight or slightly concave, not fused to valve. Stylar apex stout, linear, preapical angle absent. Aedeagus asymmetrical in posterior aspect, left subapical margin sinuate in posterior aspect, right subapical margin straight or somewhat convex in posterior aspect. Gonopore at base on right side.

FEMALE SEVENTH STERNUM.—Posterior margin shallowly excavated, median of excavation with short, produced projection bearing two short teeth (see Linnavuori 1959: Fig. 113g). Depth of excavation varies from only slightly to one-third width of segment.

TYPE.—A single female cotype bearing the labels "Martinique W.I., VII-26" and "Aug. Busck collector" was examined from the USNM.

DISTRIBUTION.—Many specimens from the following localities were examined: CENTRAL AMERICA: Honduras, Mexico (Chiapas, Guerrero, Michoacan, Oaxaca, Tamaulipas, Veracruz), Nicaragua, Panama. WEST INDIES: Antigua, Cayman Islands, Dominican Republic, Guadeloupe, Haiti, Jamaica, Montserrat, Nevis, Puerto Rico, Trinidad, and Tobago. SOUTH AMERICA: Venezuela (Guarico).

Specimens were collected from May through December and are deposited in the UPB, UCV, UKC, USNM, OSUC, and BMNH collections.

NOTE.—The types of *bidentatus*, *dilutus*, and *kinonanus* were not available for study; consequently, previous synonymies of these names under *I. tethys* were not verified. Because the types are females, it is doubtful that they can be correctly associated with males at this time.

## *Ileopeltus nanocanthus*, n. sp.

Figs. 6–10, 58, 60; Map 2

DIAGNOSIS.—*Ileopeltus nanocanthus* is near *I. tethys* and can be separated from it and other *Ileopeltus* species by the short pygoferal spine.

LENGTH.—Male 4.6–5.4 mm, female 4.8–5.3 mm.

Map 1. Distribution of *Ileopeltus tethys*.

COLOR.—Ochraceous or greenish yellow. Eye reddish brown. Crown occasionally with faint orange, median band. Pronotum with four longitudinal, faint orange bands. Forewing yellowish subhyaline, brown spots present at bases of anteapical cells and on claval area.

MALE GENITALIA.—Pygofer with ventral margin roundly produced into short spine on dorsoposterior margin, spine directed medially in ventral aspect. Plate short, anterior margin convex. Stylar apex narrowed, directed posteriorly, preapical angle absent. Aedeagus linear, asymmetrical in posterior aspect, apex with opposite curve compared to *I. tethys*. Gonopore at base on right side.

FEMALE SEVENTH STERNUM.—Posterior margin with U-shaped excavation extending half length of segment, base of excavation with small V-shaped notch, notch surrounded by light brown coloration, lateral angle rounded.

TYPE.—Male holotype, Panama, Canal Zone, Curundu, 26–30-XI-1986, B. Sieberglied collector. Four female paratypes, same data as holotype; one male paratype, Panama, Chiriqui, Rio Colorado, 1,200 m, 8°5′N, 82°43′W, 26-XII-1974, H. Wolda collector; male paratype, Panama, Panama, Las Cumbres, 17–23-II-1982, H. Wolda collector. Holotype, two paratypes with same data as holotype, and one paratype from Las Cumbres deposited in OSUC, remainder in HWC.

ETYMOLOGY.—Greek, *nano* (dwarf) and *acantha* (spine) refer to the small pygofer process.

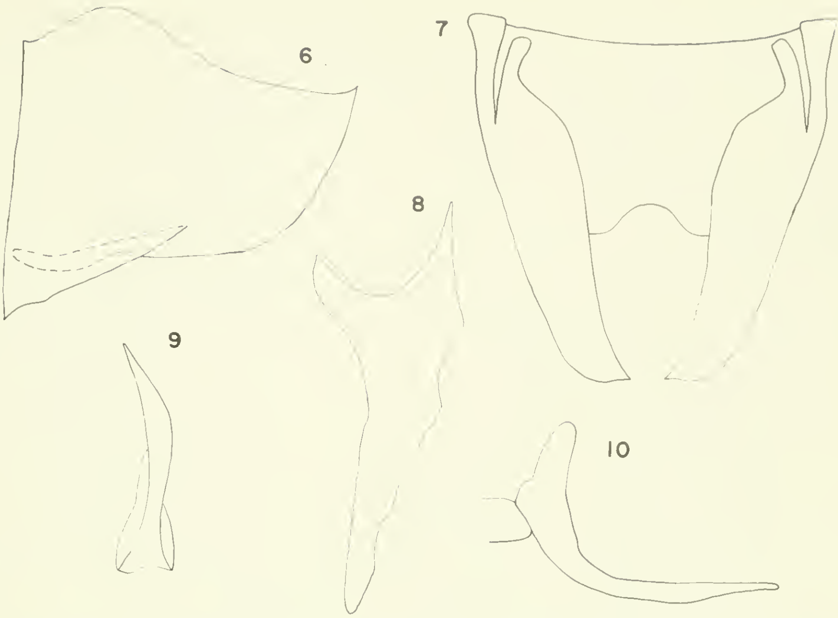
### *Ileopeltus dorsalus*, n. sp.

Figs. 11–14; Map 2

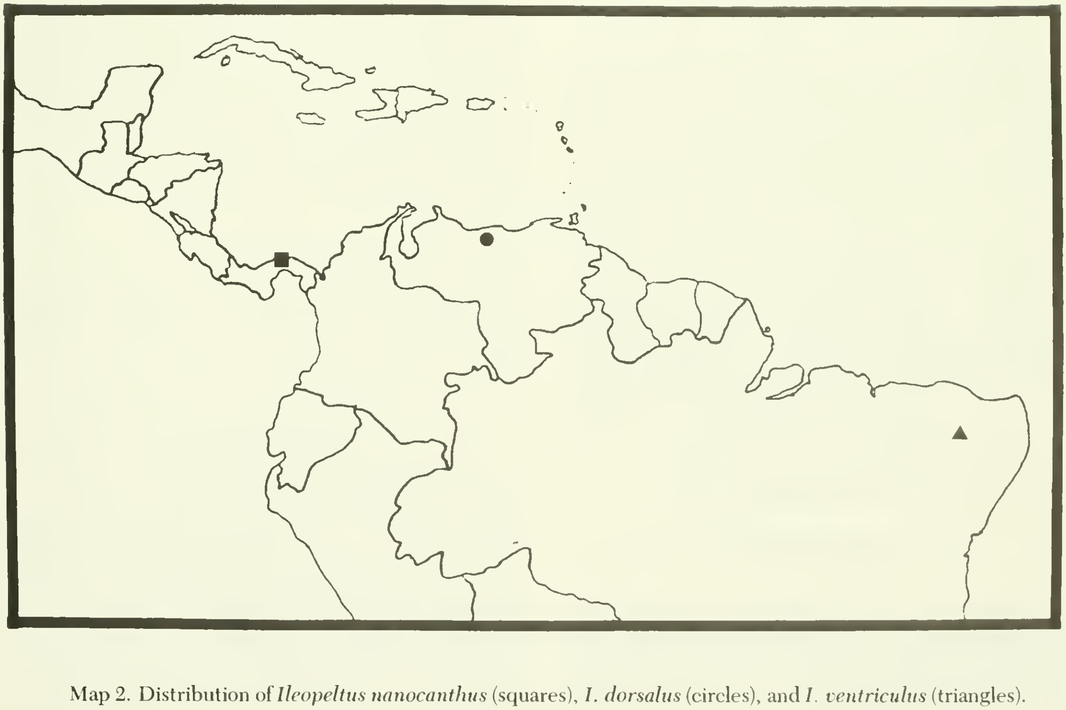
DIAGNOSIS.—*Ileopeltus dorsalus* is near *I. ventriculus* and can be separated from it by the acute, dorsally directed pygoferal spine.

LENGTH.—Male 4.4 mm, female unknown.

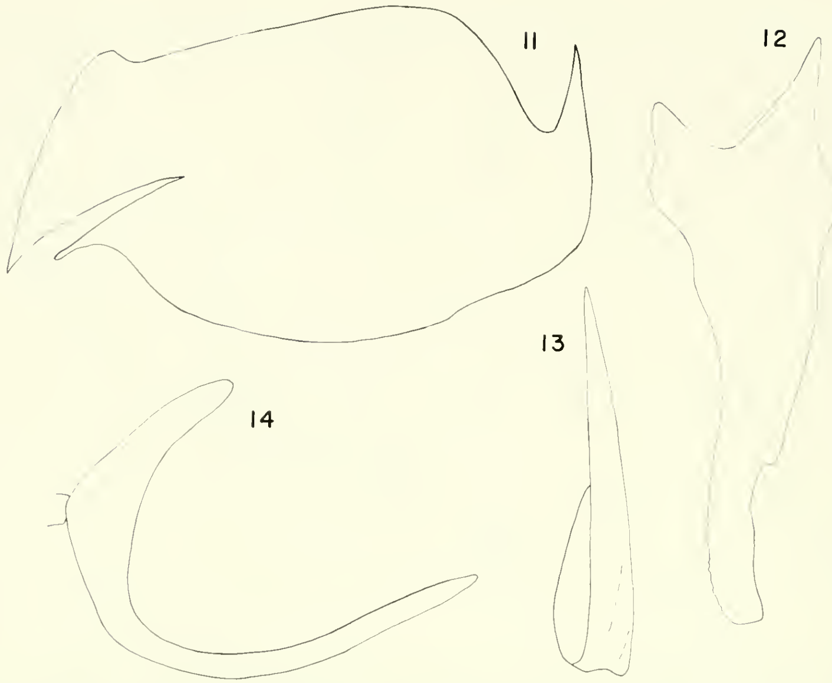
COLOR.—Ochraceous, either without dark markings or crown with light brown surrounding coronal sulcus. Eye red. Pronotum with six light brown, longitudinal bands. Scutellum with brown lateral angles. Forewing subhyaline with brown patches at base of anal




Figs. 6–10. *Ileopeltus nanocanthus*, n. sp.: 6, pygofer, left lateral aspect; 7, pygofer, ventral aspect; 8, right style, dorsal aspect; 9, aedeagus, ventral aspect; 10, aedeagus and apex of connective, left lateral aspect.



Map 2. Distribution of *Ileopeltus nanocanthus* (squares), *I. dorsalus* (circles), and *I. ventriculus* (triangles).




Figs. 11–14. *Ileopeltus dorsalus*, n. sp.: 11, pygofer, left lateral aspect; 12, right style, dorsal aspect; 13, aedeagus, ventral aspect; 14, aedeagus and apex of connective, left lateral aspect.

veins, proximal and distal ends of inner anteapical cell, and proximal end of central anteapical cell.

MALE GENITALIA.—Pygofer with posterior margin produced into dorsally directed spine, acute apically, not heavily sclerotized, small group of microsetaelike structures near middle of posterior margin. Plate triangular, lateral margin straight. Stylar apex truncate, directed posteriorly, preapical angle small. Aedeagus only slightly asymmetrical.

TYPE.—Male holotype, Venezuela, Aragua, El Limon, 22-II-1973, Malaise trap, C. J. Rosales collector. Male paratype, Brazil, Ceara, Barbalha, V-1969, M. Alvarenga, B.M. 1971-165. Holotype deposited in OSUC, paratype in BMNH.

ETYMOLOGY.—Latin, *dorso* (back) refers to the dorsally directed pygoferal spine.

*Ileopeltus ventriculus*, n. sp.
Figs. 15–18; Map 2

DIAGNOSIS.—*Ileopeltus ventriculus* is near *spinosus* and can be separated from it and other *Ileopeltus* species by the pygoferal process directed ventrally.

LENGTH.—Male 4.4 mm, female unknown.

COLOR.—Ochraceous, without distinct dark markings. Eye reddish brown.

MALE GENITALIA.—Pygofer with short, ventrally directed process inserted on posterior margin. Plate elongate, lateral margin sinuate, apex curved dorsally, bluntly rounded. Style elongate, apex linear, slightly curved laterally. Aedeagus elongate, broadly curved dorsally in lateral aspect, apex acute in posterior aspect.

TYPE.—Male holotype, Brazil, Ceara, Crato, May 1969, M. Alvarenga collector. Type deposited in BMNH.

ETYMOLOGY.—Latin, *ventricul* (belly) refers to the ventrally directed pygofer process.

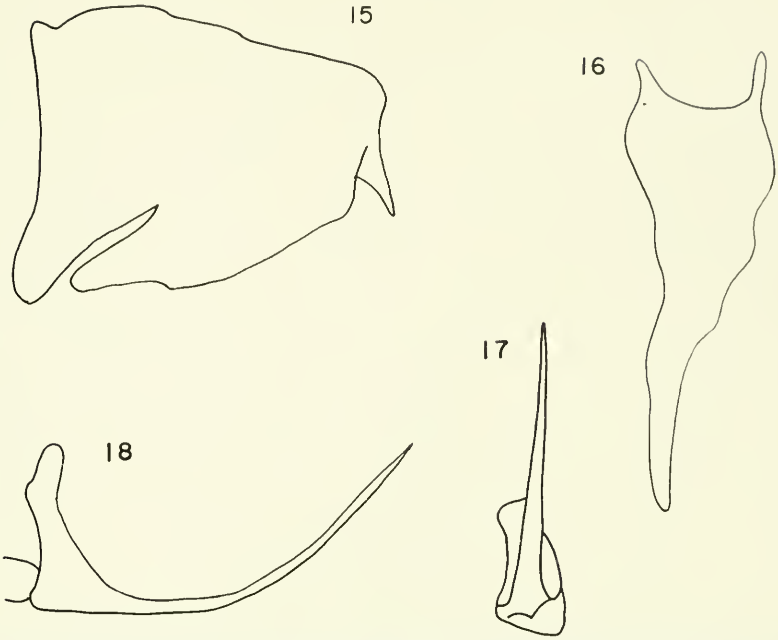
*Ileopeltus spinosus* (DeLong), n. comb.
Figs. 19–22; Map 3

*Chlorotettix spinosus* DeLong 1945:10–11.

DIAGNOSIS.—*Ileopeltus spinosus* is near *I. dorsalus* and can be separated from it and other *Ileopeltus* species by the presence of a preapical angle on the style and the unique pygoferal process.

LENGTH.—Male 5.2–5.5 mm, female unknown.

COLOR.—Greenish yellow, without dark-markings. Eye gray or greenish yellow.




Figs. 15–18. *Ileopeltus ventriculus*, n. sp.: 15, pygofer, left lateral aspect; 16, right style, dorsal aspect; 17, aedeagus, ventral aspect; 18, aedeagus and apex of connective, left lateral aspect.

MALE GENITALIA.—Pygofer with posterior margin broadly rounded apically, heavily sclerotized process inserted on posteroventral margin, directed posteriorly then curved medially. Plate with lateral margin slightly sinuate, apex elongate, pointed. Stylar apex narrowly elongate, directed slightly laterally, preapical angle roundly triangular. Aedeagus elongate, not strongly asymmetrical, narrow in ventral aspect. Gonopore on right side near base.

TYPE.—Male holotype bearing the labels "Buena Vista, Gro. [Guerrero, Mexico], 23-X-1941, 3,400 ft." and "DeLong, Good, Caldwell and Plummer" was examined from OSUC.

DISTRIBUTION.—Besides the type, three paratypes from Mazaclan, Guerrero, Mexico, 3-X-1945, were examined from OSUC.

NOTE.—DeLong (1945) reported this species from meadow grasses.

*Ileopeltus haplus*, n. sp.
Figs 23–26; Map 3

DIAGNOSIS.—*Ileopeltus haplus* is near *I. spinosus* and can be separated from it and other *Ileopeltus* species by the unique pygofer process and the wide aedeagus in ventral aspect.

LENGTH.—Male 5.3 mm, female unknown.

COLOR.—Yellowish green, without dark markings. Eye yellowish green.

MALE GENITALIA.—Pygofer with posterior margin produced into dorsally directed spine, spine not heavily sclerotized. Plate triangular, lateral margin straight, apex rounded. Stylar apex linear, preapical angle absent. Aedeagus asymmetrical, left margin forming carina in posterior aspect. Gonopore on right side near base.

TYPE.—Male holotype, [Brazil] MS [Matto Grosso du Sul], Campo Grande, 1-X-1982, W. Koller collector. Type deposited in UPB.

ETYMOLOGY.—Greek, *haplo* (simple) refers to the color of this species.

*Ileopeltus hastulus* (DeLong & Linnavuori), n. comb.
Figs. 27–32; Map 3

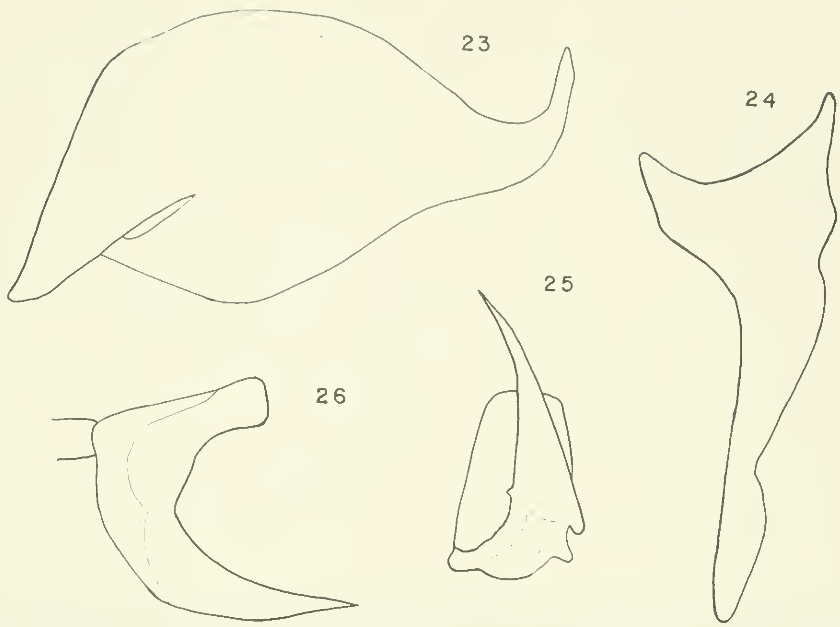
*Chlorotettix hastulus* DeLong & Linnavuori 1978:121–122.

DIAGNOSIS.—This species can be separated from other members of this genus by the long pygofer process and the aedeagus with a large gonopore.

LENGTH.—Male 5.0–5.2 mm, female unknown.


Figs. 19–22. *Ileopeltus spinosus* (DeLong): 19, pygofer, left lateral aspect; 20, right style, dorsal aspect; 21, aedeagus, ventral aspect; 22, aedeagus and apex of connective, left lateral aspect.

Map 3. Distribution of *Ileopeltus spinosus* (squares), *I. haplus* (circles), and *I. hastulus* (triangles).




Figs. 23–26. *Ileopeltus haplus*, n. sp.: 23, pygofer, left lateral aspect; 24, right style, dorsal aspect; 25, aedeagus, ventral aspect; 26, aedeagus and apex of connective, left lateral aspect.

COLOR.—Ochraceous, without dark markings. Eye grey.

MALE GENITALIA.—Pygofer with posterior margin rounded in lateral aspect, long, dorsally directed process inserted on posteroventral margin, processes crossing each other in posterior aspect. Plate with lateral margin sinuate. Style posteriorly directed, preapical angle rounded. Aedeagus with base expanded in lateral aspect, small flange present on right side in posterior aspect. Gonopore large on right side at base of shaft.

TYPE.—Male holotype bearing the label "Surumu, Roraima [Brazil], IX-1966, M. Alvarenga and F. M. Oliveira Col." has been examined from OSUC.

DISTRIBUTION.—Known from the type locality (Roraima, Brazil) and a second male specimen from Guarico, Venezuela, in USNM. This species may be restricted to the lowland tropics.

## *Ileopeltus blockeri*, n. sp.
Figs. 33–37; Map 4

DIAGNOSIS.—*Ileopeltus blockeri* is near *I. hastulus* and can be separated from it by the pygofer processes inserted near the middle in dorsal aspect.

LENGTH.—Male 4.2–4.7 mm, female unknown.

COLOR.—Ochraceous, without dark markings. Eye grey.

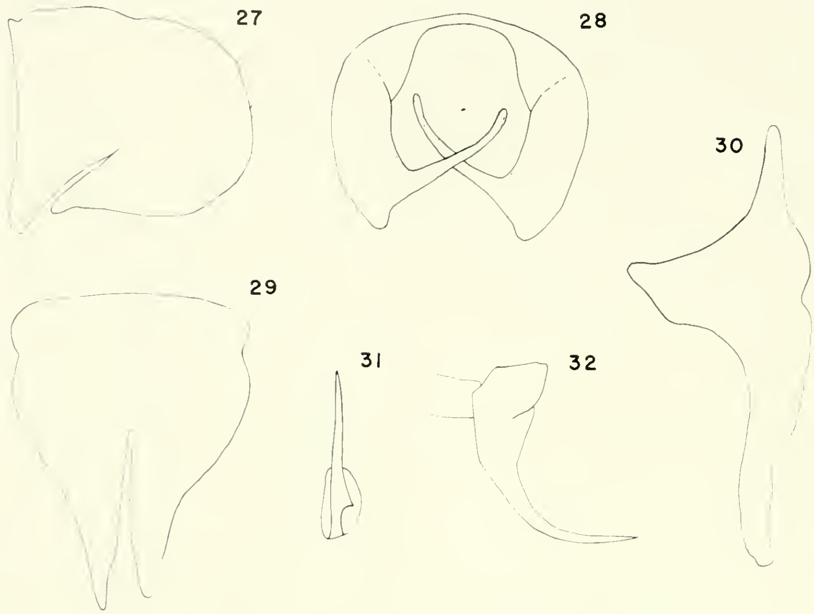
MALE GENITALIA.—Pygofer with posterior margin roundly produced, long acute process inserted on ventral margin, near middle in dorsal aspect, directed dorsally, crossing median line in dorsal aspect. Plate with lateral margin insinuate, apex narrowly rounded. Style linear, apex slightly curved laterally. Aedeagus elongate compared to other members of the genus.

TYPE.—Male holotype, Venezuela, Guarico, 10 km east of Calabozo, 18-III-1982, G. F. Hevel and J. F. Hevel collectors. Type deposited in USNM.

ETYMOLOGY.—This species is named in honor of the noted leafhopper worker, H. Derrick Blocker.

## *Ileopeltus clavatus*, n. sp.
Figs. 38–42; Map 4

DIAGNOSIS.—*Ileopeltus clavatus* can be




Figs. 27–32. *Ileopeltus hastulus* (DeLong & Linnavuori): 27, pygofer, left lateral aspect; 28, pygofer, posterior aspect; 29, plates and valve, ventral aspect; 30, right style, dorsal aspect; 31, aedeagus, ventral aspect; 32, aedeagus and apex of connective.

separated from other *Ileopeltus* species by the truncate stylar apex that is slightly constricted subapically.

LENGTH.—Male 4.2–4.4 mm, female 4.5 mm.

COLOR.—Ochraceous, without dark markings. Eye reddish brown.

MALE GENITALIA.—Pygofer with posterior margin truncate, stout process inserted on posteroventral margin in lateral aspect, apex of process crossing median line in dorsal aspect. Plate triangular, lateral margin straight, fused to valve along anterior margin. Style directed posteriorly, apex truncate, with slight subapical constriction, preapical angle absent. Aedeagus elongate, only slightly asymmetrical.

FEMALE SEVENTH STERNUM.—Posterior margin broadly convex, without excavations.

TYPE.—Male holotype, Brazil, RR [Roraima], Boa Vista, 27-VII-1952, M. Alvarenga collector. One female paratype, same data as holotype. One male paratype, Venezuela, Guarico, 10 km east of Calabozo, 18-III-1982, G. F. Hevel and J. F. Hevel collectors. Holotype and female paratype deposited in UPB and male paratype in USNM.

ETYMOLOGY.—Latin, *clavat* (clubbed) refers to the shape of the stylar apex.

*Ileopeltus aberrans* (Osborn), n. comb.
Figs. 43–46; Map 4

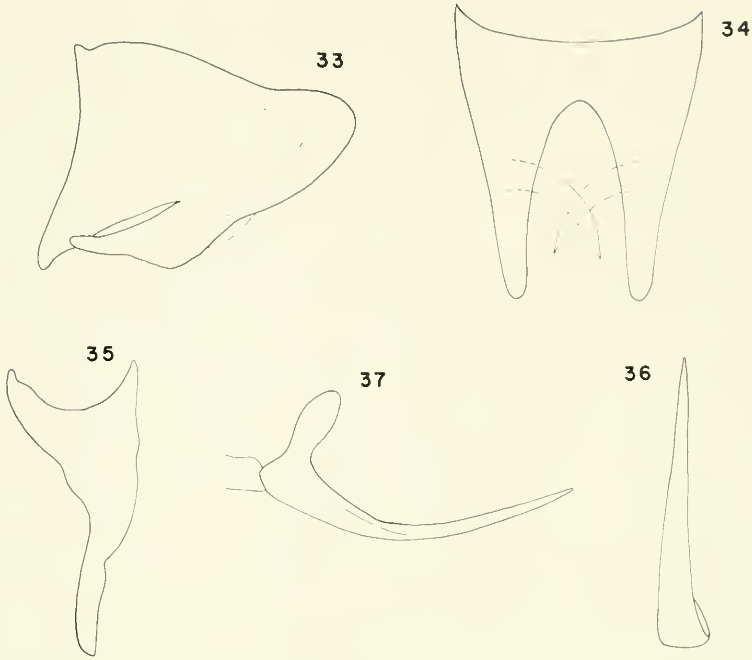
*Chlorotettix aberrans* Osborn, 1923:72–73.
*Doleranus cruzanus* DeLong & Cwikla 1984:726. New synonymy

DIAGNOSIS.—*Ileopeltus cruzanus* is related to *I. cuneus* and can be separated from it by the narrow aedeagal shaft in ventral aspect.

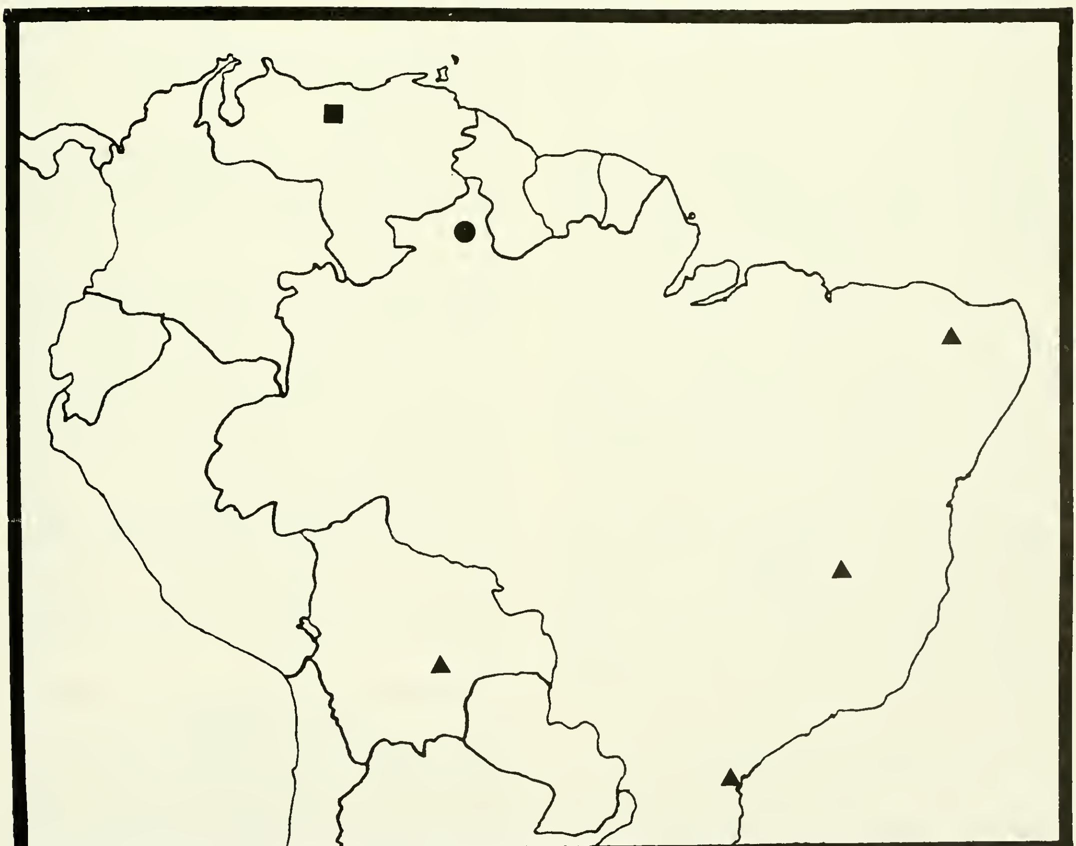
LENGTH.—Male 5.5–6.0 mm, female unknown.

COLOR.—Ochraceous. Crown with faint brown spot at apex of coronal sulcus, small triangular patch approximately halfway between sulcus and eye. Pronotum ochraceous with irregular, light brown spots on anterior margin and six light orange bands running the length of pronotum. Forewing brownish subhyaline, dark brown coloration along commissure on clavus and few brown spots on middle of wing.

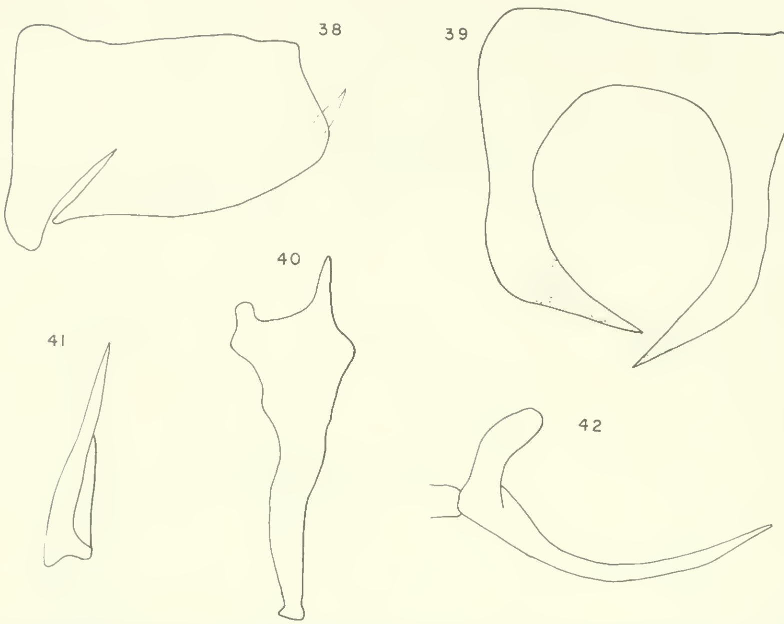
MALE GENITALIA.—Pygofer with posterior margin truncate in lateral aspect, large, curved spine on posteroventral margin, spine curves medially then posteriorly, spines overlapping




Figs. 33–37. *Ileopeltus blockeri*, n. sp.: 33, pygofer, left lateral aspect; 34, pygofer, dorsal aspect; 35, right style; 36, aedeagus, ventral aspect; 37, aedeagus and apex of connective, left lateral aspect.



Map 4. Distribution of *Ileopeltus blockeri* (squares), *I. clavatus* (circles), and *I. aberrans* (triangles).




Figs. 38–42. *Ileopeltus clavatus*, n. sp.: 38, pygofer, lateral aspect; 39, pygofer, dorsal aspect; 40, right style, dorsal aspect; 41, aedeagus, ventral aspect; 42, aedeagus and apex of connective, left lateral aspect.

at middle. Plate triangular, slightly longer than pygofer, lateral margin straight, not appearing fused to valve, two rows of setae present, one row of macrosetae plus row of small setaelike structures on lateral margin. Stylar apex elongate, preapical angle absent. Aedeagus U-shaped in lateral aspect, acute apically. Gonopore basal, on right side of shaft.

TYPE.—Male holotype bearing the labels "Januaria, Minas Gerais, Brazil," "Dec 17, 1907" and "Carn. Mus. Acc. 3702" was examined from CMNH. The holotype of *cruzanus* DeLong & Cwikla from Santa Cruz, Bolivia, was examined from OSUC and found to match the type of *I. aberrans*.

DISTRIBUTION.—In addition to the type locality and Santa Cruz, Bolivia, two males from Ceara and Sao Paulo, Brazil, were examined from BMNH. The specimen from Sao Paulo was collected from grass in a cloud forest. Collecting dates included late February and May.

*Ileopeltus cuneus* (DeLong & Martinson), n. comb.
Figs. 47–50; Map 5

*Chlorotettix cuneus* DeLong & Martinson 1974:265.

DIAGNOSIS.—*Ileopeltus cuneus* is close to *I. cyclops* and can be separated from it by the asymmetrical aedeagus and the unique pygofer process.

LENGTH.—Male 4.8 mm, female unknown.

COLOR.—Ochraceous. Crown with median triangular patch at apex of coronal sulcus, faint brown spot halfway between sulcus and each eye.

MALE GENITALIA.—Pygofer produced into long process, curved medially then dorsally. Plate rounded apically, lateral margin slightly convex. Stylar apex linear, spatulate, U-shaped notch subapically on laterally surface in dorsal aspect. Aedeagus slightly expanded in posterior aspect, right side with two toothlike projections near base.

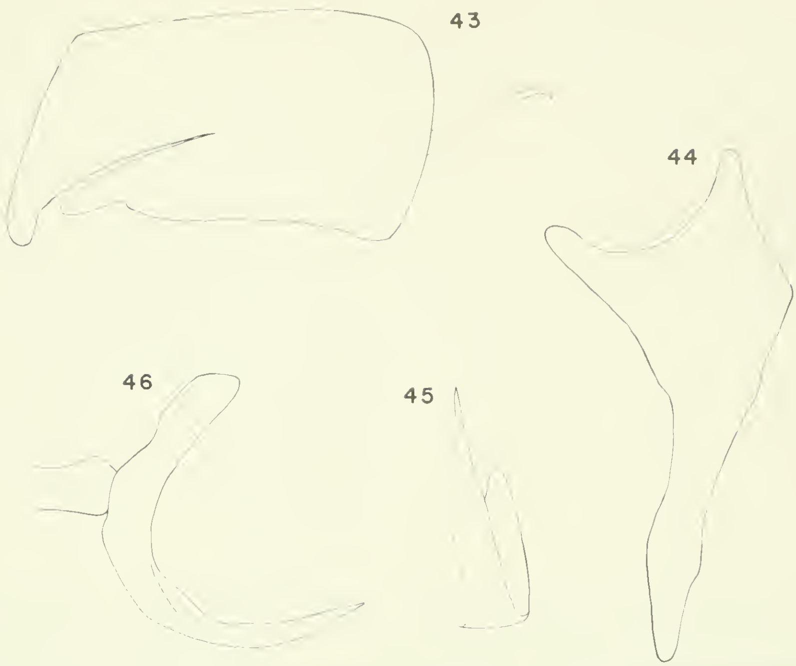
TYPE.—Male holotype bearing the labels "Piracicaba, Sao Paulo, Brazil, 1-4-1966," "collr. C. A. Triplehorn," and "Blacklight trap" was examined from OSUC.

DISTRIBUTION.—Known only from the holotype.

*Ileopeltus cyclops* (Linnavuori), n. comb.
Figs. 51–55; Map 5

*Doleranus cyclops* Linnavuori 1959:275–276.

DIAGNOSIS.—This unique species can be separated from other *Ileopeltus* species by the median spot on the crown and the unique stylar apex.




Figs. 43–46. *Ileopeltus aberrans* (Osborn): 43, pygofer, left lateral aspect; 44, right style, dorsal aspect; 45, aedeagus, ventral aspect; 46, aedeagus and apex of connective, left lateral aspect.

LENGTH.—Male 4.9 mm, female unknown.

COLOR.—Ochraceous. Crown with median triangular brown patch. Eye gray.

MALE GENITALIA.—Pygofer with posterior margin produced into acute process posteriorly directed then curving medially, sclerotized. Plate short, rounded apically. Stylar apex acute, distal third abruptly curved laterally, preapical angle absent. Aedeagus only slightly asymmetrical, shaft narrow in posterior aspect.

TYPE.—Male holotype bearing the labels "Loreto, Missiones [*Lapsus calmi* for Misiones? Possibly from Corrientes], ARG [Argentina] XII-4-1931, A.A. Ogoblin" and "collected at light" has been examined from USNM.

DISTRIBUTION.—Known only from the holotype.

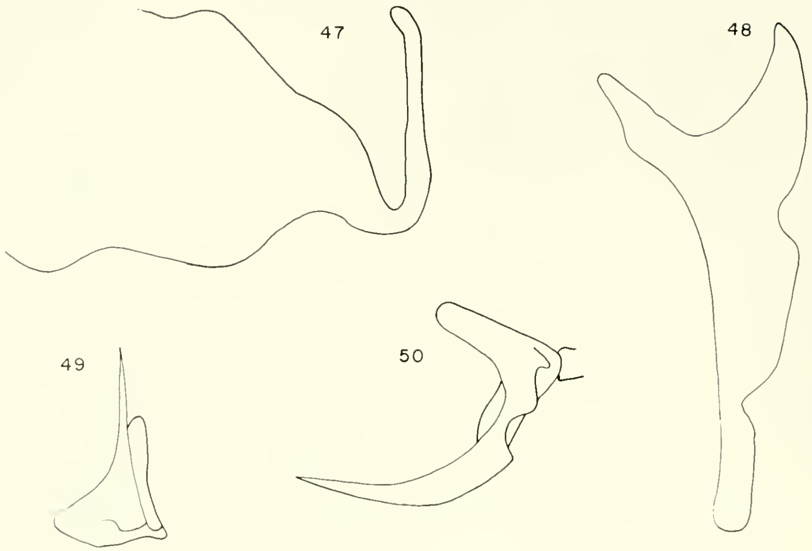
## Cladistic Relationships among the Species

Biological classifications should be based on hypothesized relationships estimated by cladistic (or phylogenetic) analyses (Hennig 1966). Such analyses are dependent upon the determination of plesiomorphic and apomorphic character states. Hypotheses of character polarity are accomplished by comparing the taxa under question with their outgroup. *Ileopeltus* is thought to be closely allied to *Chlorotettix* by nature of both having the crown completely microsculptured. Because of this single synapomorphy, *Chlorotettix* is considered the sister-group to *Ileopeltus*.

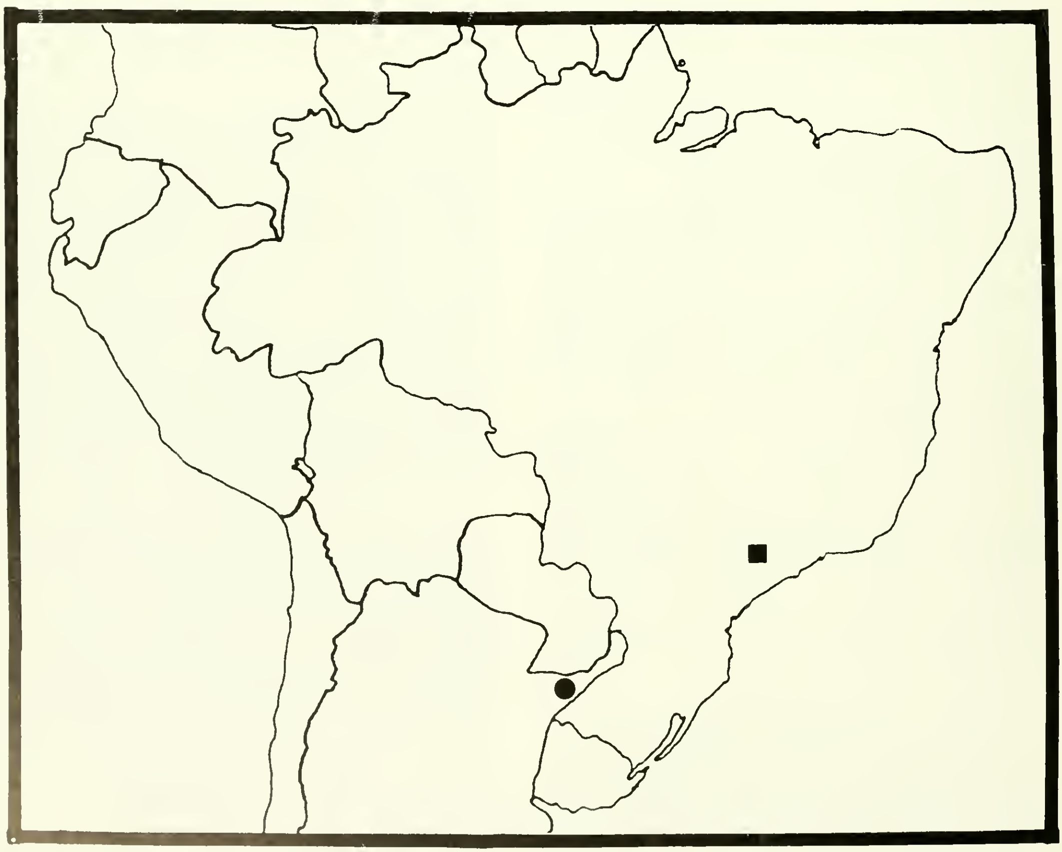
Twelve binary characters were chosen for the cladistic analysis and are summarized in Table 1. The resulting data matrix (Table 2) was analyzed by means of phylogenetic analysis using the parsimony (PAUP) program developed by Swofford (1985).

The paucity of characters for *Ileopeltus* species, I believe, is the result of a generalized reduction in complexity of characters. This becomes immediately obvious when the male genital structures are examined, e.g., the aedeagus without processes. These reduced characters most assuredly obscure the interrelationships among the species and possibly at higher levels. Even with this reduction, most of the characters used in this analysis were genitalic and are discussed below.

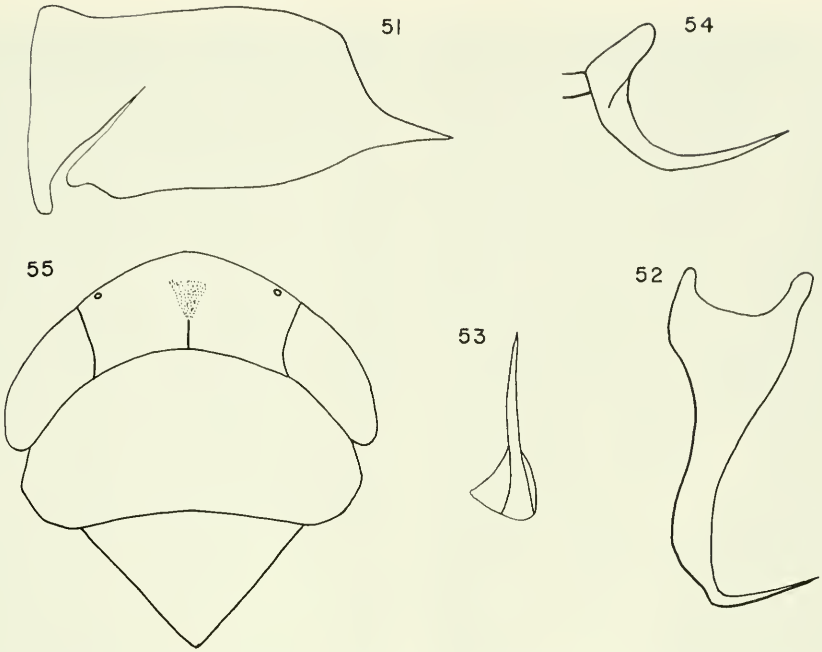
The hypothesized cladogram is presented in Figure 56. The most primitive lineage contains the species *I. tethys* and *I. nanocanthus*,




Figs. 47–50. *Ileopeltus cuneus* (DeLong & Martinson): 47, pygofer with anterior portion damaged, left lateral aspect; 48, right style, dorsal aspect; 49, aedeagus, ventral aspect; 50, aedeagus and apex of connective, right lateral aspect.



Map 5. Distribution of *Ileopeltus cuneus* (squares) and *I. cyclops* (circles).




Figs. 51–55. *Ileopeltus cyclops* (Linnavuori): 51, pygofer, left lateral aspect; 52, right style, dorsal aspect; 53, aedeagus, ventral aspect; 54, aedeagus and apex of connective, left lateral aspect; 55, head, pronotum, and scutellum, dorsal aspect.

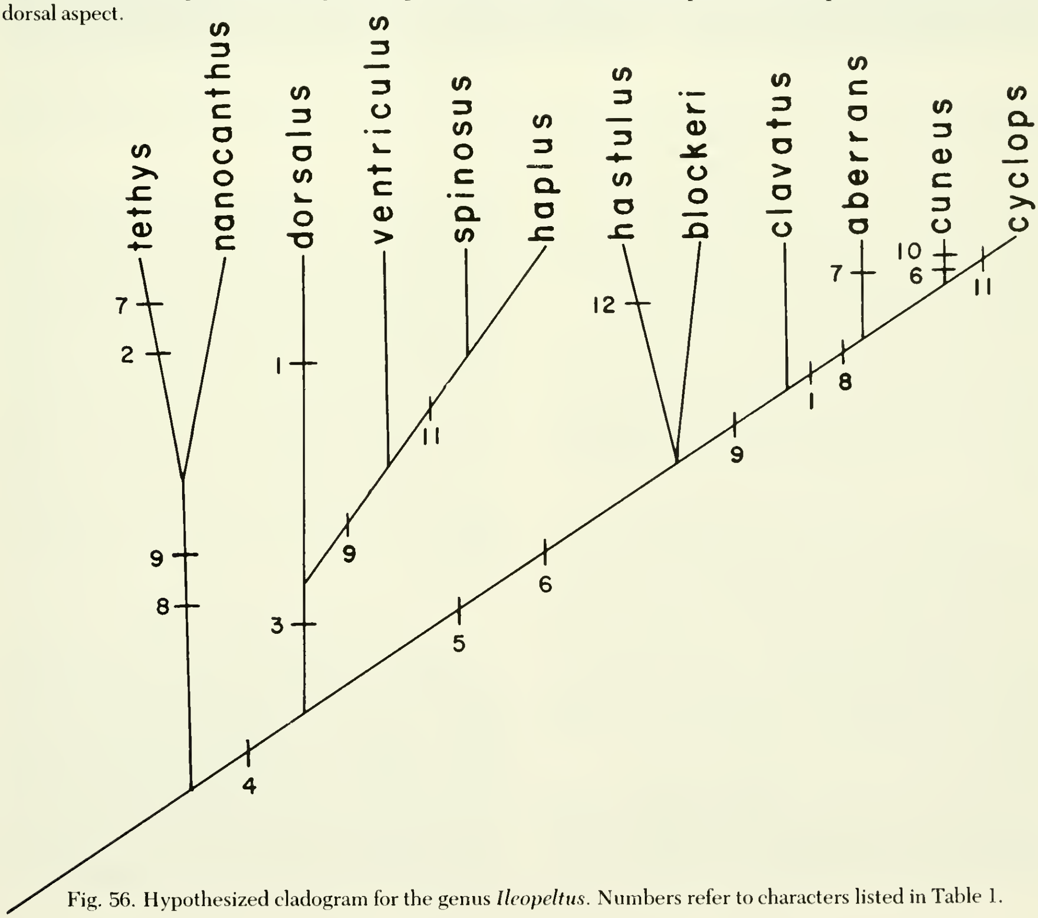



Fig. 56. Hypothesized cladogram for the genus *Ileopeltus*. Numbers refer to characters listed in Table 1.

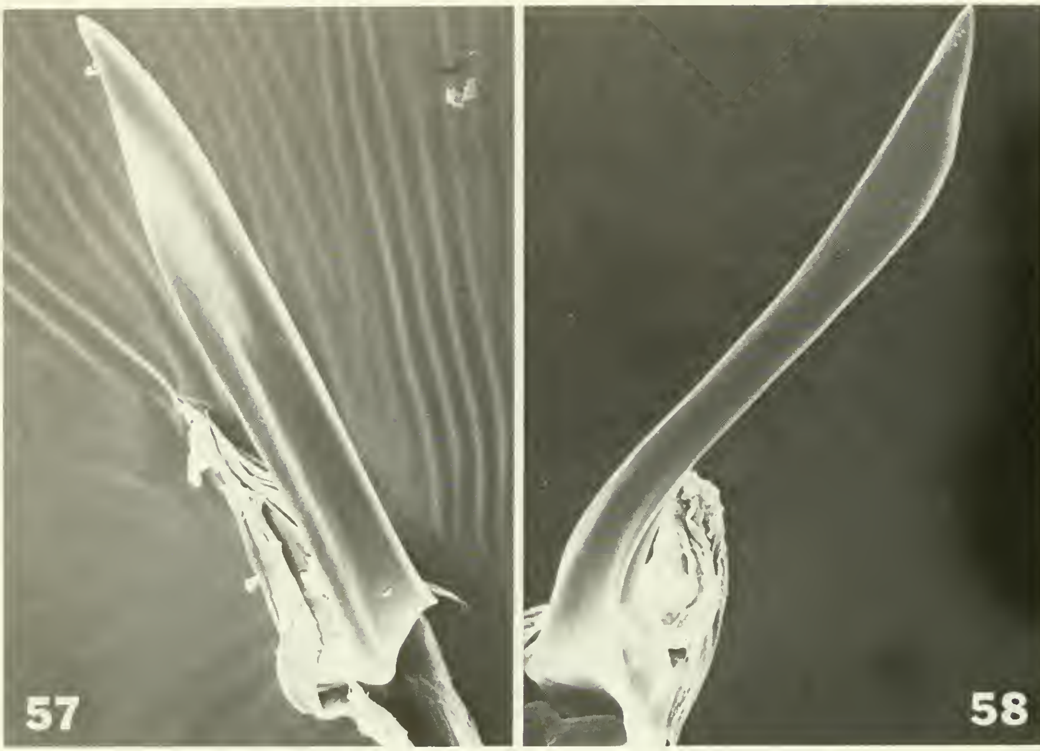



Fig. 57. *Ileopeltus tethys* (Van Duzee), aedeagus, ventral aspect. Fig. 58. *I. nanocanthus*, n. sp., aedeagus, ventral aspect.

which share the synapomorphy of the concave plate and the style with the preapical angle absent. Both characters are homoplastic and are found throughout the cladogram. The remaining species have a distinct process.

Of those *Ileopeltus* species with prominent pygoferal processes, two major lineages are hypothesized. One contains those individuals with stout pygoferal processes; the other is defined by long, heavily sclerotized processes.

The lineage with stout pygoferal processes contains four species. *Ileopeltus dorsalus* has a median black patch on the crown, while the remaining three species have the preapical angle of the style absent, a homoplastic character found throughout the cladogram. *Ileopeltus haplus* and *I. spinosus* have their stylar apex truncate, another homoplastic character.

The lineage that is defined by the long sclerotized process is also supported by the processes curved medially, a character which is later reversed. The lineage itself is represented by an unresolved trichotomy containing *I. hastulus*, *I. blockeri*, and the remaining *Ileopeltus* species. *Ileopeltus hastulus* is defined by the autapomorphy of a large gonopore. The remaining four species have the preapical angle of the style absent. As mentioned before, this is a homoplastic character.

*Ileopeltus aberrans*, *I. cyclops*, and *I. cuneus* have a median black patch on their crown and the lateral margin of their plate concave. Both characters are homoplastic. Only autapomorphic characters define these species.

## Acknowledgments

I thank the following individuals and their associated institutions for allowing me to examine specimens under their care: M. D. Webb, Department of Entomology, British Museum (Natural History), London (BMNH); C. W. Young, Section of Entomology, Carnegie Museum of Natural History, Pittsburgh (CMNH); C. A. Triplehorn, Department of

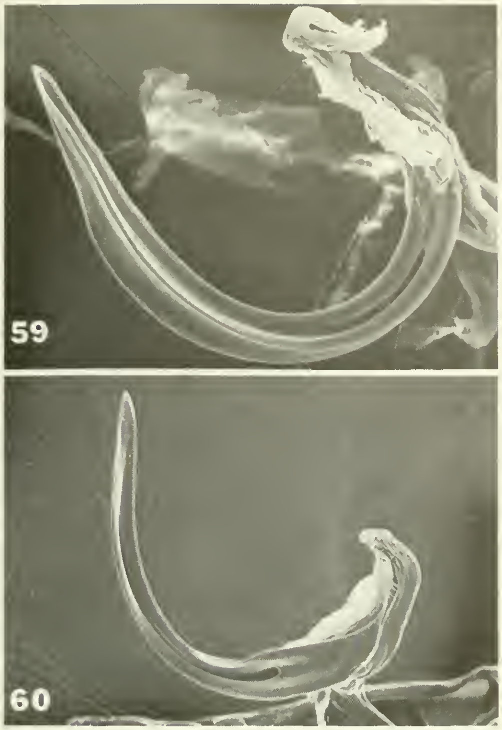


Fig. 59. *Ileopeltus tethys* (Van Duzee), aedeagus, right lateral aspect. Fig. 60. *Ileopeltus nanocanthus*, n. sp., aedeagus, right lateral aspect.

Entomology, Ohio State University, Columbus (OSUC); the late Francisco Jose Fernandes-Yepez, Facultad de Agronomia, Universidad Central de Venezuela, Maracay (UCV); Paul H. Freytag, Department of Entomology, University of Kentucky, Lexington (UKC); K. M. Rocha Zanol, Universidade Federal do Parana, Curitiba, Brazil (UPB); J. P. Kramer and R. Froeschner, Department of Entomology, Smithsonian Institution, Washington (USNM); H. Wolda, Smithsonian Tropical Research Institute, Balboa, Republic of Panama (HWC). H. Derrick Blocker (Kansas State University), P. H. Freytag (UKC), Sam Stribling (USNM), and G. M. Chippendale (University of Missouri, Columbia) kindly criticized an earlier draft of this manuscript. Niki K. J. Miller (Ohio State University) skillfully executed the habitus drawing. Special thanks are extended to Paul W. Oman, whose works on leafhopper systematics have proved to be most inspiring.

TABLE 1. Characters, presumed plesiomorphic and apomorphic states for *Ileopeltus* species, and numbers that refer to character distribution presented in Table 2 and Fig. 56.

| Character | Plesiomorphic | Apomorphic |
|---|---|---|
| 1. Coloration | unmarked | crown marked with median triangular patch |
| 2. Pygoferal processes | absent | present |
| 3. Pygoferal processes elongate | no | yes |
| 4. Pygoferal processes stout | no | yes |
| 5. Pygoferal processes long and heavily sclerotized | no | yes |
| 6. Pygoferal processes strongly curved medially | no | yes |
| 7. Plates fused to valve | no | yes |
| 8. Plates with lateral margin | straight | concave |
| 9. Style with preapical angle | present | absent |
| 10. Stylar apex | stout | narrow |
| 11. Stylar apex | rounded | truncate |
| 12. Gonopore | small | large |

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TABLE 2. Data matrix used in constructing a cladogram for *Ileopeltus*. Characters number refers to information in Table 1: 0, plesiomorphic; 1, apomorphic.

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chlorotettix* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *I. cuneus* | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *I. cyclops* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *I. aberrans* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *I. blockeri* | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *I. hastulus* | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *I. tethys* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *I. nanocanthus* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *I. haplus* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *I. dorsalus* | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *I. clavatus* | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *I. spinosus* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *I. ventriculus* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |

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# SOME ASPECTS OF THE BIOLOGY, MORPHOLOGY, AND EVOLUTION OF LEAFHOPPERS (HOMOPTERA: CICADELLOIDEA AND MEMBRACOIDEA)

J. W. Evans[1]

ABSTRACT.—This article summarizes some observations of a varied nature on the biology, morphology, and evolution of the Cicadelloidea (Cicadellidae, Hylicidae, Eurymelidae) and Membracoidea (Membracidae, Aetalionidae, Biturritidae, Nicomiidae). These observations, made over a period of more than half a century, have previously been recorded at different times, but lie buried in the literature. It is hoped that their interest will justify repetition and draw attention to some promising lines of research.

## BIOLOGY

### Food Plant Associations

As Southwood (1961) has pointed out, insects have a particularly close association with plants belonging to the predominant flora of the time. Thus, most Australian cicadelloids feed on eucalypts and numerous membracids on acacias. Of particular interest are relict insects that feed on representatives of ancient floras. Examples are *Koebelia californica* Baker on conifers in California and *Cornutipo* spp. (Eurymelidae) on representatives of the Proteaceae in Australia. The Cephalelini, a tribe of the Ulopinae which have an Antarctic distribution, provide another example, for their feeding seems to be restricted to an ancient family of plants, the Restionaceae, in Australia, South Africa, and New Zealand.

Changes of food plants have recently occurred in the Tartessinae (Cicadellidae). These are primarily eucalypt feeders, but some have become adapted to living in tropical rain forests and have taken to feeding on other kinds of trees (F. Evans 1981).

### Sound Production and Courtship

Ossiannilsson, in his notable study of the "songs" of Homoptera, was the first to draw attention to the presence of tymbals in insects of both sexes belonging to the Cicadelloidea, Cercopoidea, and Cicadoidea (Ossiannilsson 1949). Previously, I had noted the presence of structures that I described as "resembling tymbals" on the first abdominal segment of *Darthula hardwickii* Gray and *Aetalion reticulatum* Linnaeus (Evans 1946b). In his discussion of the function of the songs of various Auchenorrhyncha, Ossiannilsson described some as being "calls of courtship." Subsequently, I noted the presence of well-developed tymbals in nymphs belonging to every instar but the first in both sexes of *A. reticulatum* (Evans 1957). As, presumably, nymphal song cannot have a sexual significance, it may serve an assembling purpose since aetalionids are gregarious insects. However, amongst the Eurymelidae, which are likewise gregarious, I have been unable to find any trace of tymbals. Nevertheless, prior to mating, eurymelids indulge in a prolonged courtship (Evans 1931).

Tymbal sound production occurs among representatives of all the superfamilies of the Auchenorrhyncha, and even in the Cicadoidea it is not confined to one sex since females of *Tettigarcta* can "sing." Thus, it must have been a feature acquired in early Mesozoic, if not Palaeozoic, times (Evans 1941). Moreover, it would seem that during the early Mesozoic some Auchenorrhyncha were capable of stridulation. This is supposed because some Upper Triassic Homoptera (e.g., *Eoscartoides bryani* Evans) have stridulatory areas on the proximal costal area of their tegmina (Evans 1961).

### Oviposition

When ovipositing, the majority of leafhoppers insert their eggs into plant tissue, either singly or in batches. In the latter case, the eggs are covered with secretions that harden

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on exposure to the air. The eggs of aetalionids and of some bitturitids and membracids are contained in oothecae situated on the surface of the plants. Because the Aetalionidae are an ancient group of insects, it might be thought that such a method of oviposition predated egg insertion in plant tissue. However, this is improbable, as the last-named method is shared with insects belonging to the superfamilies of the Auchenorrhyncha; and eggs, whether laid inside plants or on their surface, are equally subject to heavy parasitism.

### Gregariousness and Ant Attendance

While all eurymelids and aetalionids, many membracids, and possibly all bitturitids are gregarious, so far as I am aware, no cicadellids have this behavior pattern. Since female membracids sometimes remain with their eggs after oviposition, some authors, such as Haviland (1925), have credited them with maternal care. Eurymelids of both sexes have been recorded as remaining with their eggs for a period. It is possible that the gregarious habit in this family may be associated with the fact that their nymphs, unlike those of other leafhoppers, lack the ability to jump.

It would seem that all gregarious leafhoppers are ant attended, but the Pogonoscopini, a tribe of the Eurymelidae, are the only ones that have developed the characteristics of true myrmecophiles; i.e., they have unusually long legs and small eyes and live in the nests of ants (Evans 1966).

## MORPHOLOGY

### Color and Size

Previously, I have suggested that early leafhoppers were brown, as, for instance, is *Darthula hardwickii*, and that green was the first alternative color to be acquired (Evans 1966). Later evolutionary developments have given rise to insects that may be predominantly black and have, or lack, yellow, red, or occasionally bluish markings. Some Cicadellidae from Madagascar have striking color pattern differences (Evans 1953). In others, species occur that have identical male genitalia and comprise populations with differing, but stable, color patterns (e.g., *Eurymela fenestrata* Le Peletier & Serville) (Evans 1933). Then, some species have individuals with a very variable color pattern (e.g., *Eurymeloides punctata* [Signoret]) (Evans 1966).

The largest known leafhopper, the aetalionid *Darthula hardwickii* Gray, has a length of 28 mm, of which the apical 12 mm in both sexes consists of the prolonged ninth abdominal segment. The smallest leafhoppers are comprised in the Typhlocybinae (Cicadellidae), some species of which are no more than 2 mm long. Evolutionary development seems to be frequently accompanied by increase in size. Thus, for example, in the Eurymelidae, the largest species are seemingly the most recently evolved (e.g., *Eurymelops generosa* [Stal]).

The two sexes of Cicadelloidea usually resemble each other in coloration and size. An exception in respect to color is provided by the sole representative of the Tartessinae to occur in New Caledonia. This insect, *Calotartessus stalii* (Signoret), has males that are largely black and females that are predominantly brown. In regard to size, the Stenocotini (Ledrinae) have males that are considerably smaller than females.

### The Head

The most puzzling feature of the heads of Hemiptera is associated with the origin of their feeding apparatus. Insects in some other orders feed by suction, but with all these the nature of the transition from mandibulate to haustellate mouthparts can be readily understood.

Previously, I have suggested that, though the ocelli are on the crown in representatives of the relict subfamily, the Ulopinae, this condition is a secondary one. If this is correct, even though insects with ventral ocelli do not seem to be disadvantaged, such a change of position would seem to be an adaptive one.

Other primitive features of leafhopper heads are the presence of a sensory pit on the maxillary plates, which may possibly be derived from the maxillary palp (Evans 1973), and the complete separation of the maxillary plates from the genae.

### Male Genitalia

The male genitalia of insects are more subject to change than any other parts of their bodies. For this reason, they are extensively used for species recognition. The nature and the extent of observable differences between the aedeagi of closely related insects vary

widely and range from slight and constant to considerable and variable ones. The subgenital plates and accessory processes are also subject to considerable change of shape.

While male genitalia differences are useful for species separation and genus recognition, they are sometimes also helpful for family recognition purposes. Thus, for example, while within the Cicadellidae the aedeagus invariably arises from a basal connective situated between the paired parameres, in the Eurymelidae it lacks any association with the basal plate and the parameres.

Inasmuch as simple male genitalia serve the same purpose as complex ones and presumably in an equally satisfactory manner, and the structure of female genitalia is constant, it is difficult to understand the nature of the advantages conferred by increasingly complex male genitalia unless female insects avoid mating with males that have the wrong "key."

### Adaptive Characters

In addition to the ocelli noted above, other adaptive characters among leafhoppers are to be found in the Stenocotini, an endemic Australian subfamily of the Ledrinae, and in the Eurymelidae. Stenocotids, which live under bark of eucalypts, are flattened insects, and their nymphs are paper thin. While most eurymelids are wedge-shaped, one species, *Platyeurymela semifascia* (Walker), which, like stenocotids, lives under bark, is oval in shape and convex.

Alary dimorphism and polymorphism are of widespread occurrence in the Heteroptera, they are rare in the Homoptera-Auchenorrhyncha, and in the Cicadellidae they would seem to be particularly associated with insects living at high altitudes or in a marsh environment. Thus, *Monteithia* spp. (Monteithiini, Ulopinae), which live at high altitudes in New Guinea, and of which fully winged insects have not been recorded, have males that differ from females in the extent to which their wings are foreshortened (Evans 1968). Then, in Cephalelini, which inhabit both alpine and low-level marsh environments, both sexes occur in a flightless and a fully winged condition. Some other leafhoppers with both brachypterous and fully winged individuals are *Taslopa montana* Evans (Ulopini, Ulopinae), *Chiasmus varicolor* (Kirkaldy) (Deltocephalinae), and *Euacanthella* sp. (Euacanthellinae).

The best-known examples of the acquisition of morphological features among leafhoppers, which are seemingly of nonadaptive significance, are to be found among the Membracidae. This phenomenon has been discussed by many authors (e.g., Haviland 1925) who observed these insects in the territory then known as British Guiana. She pointed out that the early stages of exaggerated pronotal development in insects, which, in their extreme form, were either cryptic or mimetic, cannot have conferred any protective advantage, and yet the insects survived. Moreover, the pronota of many membracids seem to lack any degree of protective significance.

Above I have suggested that the extreme differences found among leafhoppers belonging to the genus *Colloborrhis* Germar in Madagascar may have been initiated by "explosive speciation." I have also formerly suggested that the same phenomenon may have occurred among Membracidae isolated in the Neotropical Region during Tertiary times (Evans 1959). This is because, though doubtless enlarged pronota were a membracid characteristic before this isolation took place, it is in South America only that the evolution of such a range of bizarre forms took place.

The development in leafhoppers of bizarre structures, which apparently lack adaptive significance, is not confined to changes in the shape of the prothorax. These occur also in the heads of leafhoppers, as, for example, in those of *Cornutipo tricornis* Evans, *Listrophora evansi* Evans, and *Wolfella caternaulti* Spinola (all illustrated in Evans 1975a).

## EVOLUTION

### Fossils and the Classification of Recent Forms

An abundance of wings of Homoptera has been found in Permian and Triassic strata in both the northern and southern hemispheres. These seem to provide evidence that all the existing superfamilies of the Auchenorrhyncha were already differentiated by Triassic and possibly Permian times. If this suggestion is valid, it provides an example of unusual evolutionary stability (Evans 1964).

In the forewings, or tegmina, of some Upper Permian Homoptera (e.g., *Homaloscytina plana* Tillyard) six veins support

their apices. These are as follows: R1b, Rs, M1, M2, M3, and M4. In some recent Cicadelloidea, only four veins serve the same purpose, and it is of interest to note that the identity of these is different in each of the comprised families. Thus, in the Hylicidae, they are R1b, Rs, M1+2, and M3+4+CuA; in the Eurymelidae, R1, M1+2, M3+4, and CuA; and in the Cicadellidae, R1b, Rs+M1+2, M3+4, and CuA. This circumstance would seem to provide evidence of the separate, direct derivation of insects comprised in the leafhopper families from a common ancestral stock (Evans 1949, 1964). The recently found fossil insect placed in a new Homoptera family, the Jascopidae, belongs in my opinion to the Cicadellidae (Evans 1972).

## Parallel Evolution

The most striking example of parallel evolution in the family Cicadellidae is provided by the resemblance between insects comprised in the Cephalelini (Ulopinae) and the Paradorydiini (Hecalinae). Leafhoppers in both tribes have species with short, triangular heads and others with long, narrow ones, the complete insect being seedlike in appearance. While the Paradorydiini, unlike the Cephalelini, do not feed on the rushlike Restionaceae, some have been recorded from "rushes" growing in marshes. The Ulopinae and the Hecalinae are not closely related and probably were differentiated during different geological periods, the former being of Mesozoic and the latter possibly Tertiary origin.

## Explosive Speciation

Above I have mentioned an instance of supposed "explosive speciation" that has occurred in Madagascar with leafhoppers belonging to the genus *Coloborrhis* Germar (Ulopini, Ulopinae). The type species of the genus, *C. corticina* Germar, has an extensive distribution in Africa from where no other species has been recorded. It is established also in Madagascar, from where no less than 16 other species, which could equally well be regarded as belonging to separate genera, have been described. These differ strikingly from one another in characters of the head and thorax. Thus, the head may be rounded anteriorly, or narrowly, or broadly spatulate, and it may have differently shaped prominences on the crown. Then, the pronotum may have a pair of lateral prominences of varying size, or be laterally humped, and it may be widest either anteriorly or posteriorly, while the scutellum may be of normal size or raised into a large, vertical crest. The tegmina may have basic cicadellid, or reticulate, venation. One species (*C. rugosa* Evans) has a characteristic shared only with the tegmina of Permian and Triassic Homoptera. This is the proximal arching of vein CuA so that it makes contact with vein M. Finally, the hind tibae may be narrowly rectangular in section, or broadly spatulate. It is of interest to note that some of the characteristics listed above are shared with the Ledrinae, while others are of a membracidlike nature (Evans 1953, 1959).

## Supposed Sympatric Speciation

During 1959 a symposium was held in Melbourne to celebrate the centenary of the Royal Society of Victoria. Its proceedings were later published under the title "Evolution of living organisms." At the end of the paper I contributed to this symposium (Evans 1962), I said:

> The concept of sympatric speciation is at the present time almost universally discredited and any mention of it, even as a possibility, might seem to have no place in a contribution purporting to be scientific. This is especially so when, as in the case of the present instance, a suggestion is made that is unsupported by experimental evidence. Nevertheless, in my opinion, it is possible that sympatric speciation may take place within a particular group of leafhoppers, the Typhlocybinae, and the reason for this opinion is because amongst these insects discontinuities between populations of an ecological and ethological nature would seem to be more readily capable of achievement than isolation of a geographical nature.
>
> Typhlocybids, which are of world-wide distribution, are particularly well represented in the Holarctic Region. They range in length from 2–4 mm. This group comprises some hundred genera, several of which contain many hundreds of distinct species. These leafhoppers differ greatly in the extent to which they are restricted in their feeding requirements. Some feed, mate and breed only on a single species of plant or on a limited range of related plants. Others have wider feeding habits. The mere fact that related species have different ranges of food plants implies an ability, on occasion, to become accommodated to a new diet.
>
> Mention has already been made of the songs of Homoptera and it may be of significance that typhlocybids have unusually large apodemes for the support of their tymbal muscles and hence, presumably, are particularly vocal. It is accordingly suggested that an isolating factor which may have enabled the evolution of large numbers of sympatric species might be the synchronization of the acquisition of a new call note with that of a new food plant.
>
> The reason it has been suggested that it is improbable

that geographical isolation has been the principal factor enabling prolific speciation to take place among typhlocybids is because their small size and swarming habits make them particularly liable to transport in the upper air and hence to rapid and wide dispersal.

My views on the above matter have not changed during the 25 years that have elapsed since I first expressed them.

## Some Characteristics of Island and Montane Faunas

When the gene flow of insects is restricted following the isolation of small initial populations, the process of evolution is often accelerated. Mention has already been made of developments that have occurred on the island of Madagascar following the presumed isolation of a population of the ulopid *Coloborrhis corticina*. The occurrence of aberrant leafhoppers is not confined to large islands. Thus, on Juan Fernández Island there occurs possibly the most grotesque of all leafhoppers, *Evansiola kuscheli* (China). The head of this species is twice as wide as long, and, when observed from above, projects laterally considerably beyond the sides of the rest of the body (Evans 1975a).

Montane faunas in Australia and New Guinea comprise survivors from a time when prevailing climates were cooler than at present and from immigrant species belonging to later evolved groups. Examples belonging to the first category are provided by *Taslopa montana* Evans (Ulopinae, Ulopini), which has been recorded only from high altitudes in Tasmania and southeastern Australia, and *Monteithia* spp., which inhabit high-level environments in New Guinea (Evans 1966, 1968). A leafhopper in the second category is *Austroagalloides rosea* Evans (Austroagalloidinae) (Evans 1966).

## Relict Characteristics

The relict characteristics of leafhoppers can be recognized by making a comparison of those features in which presumed recently evolved forms differ from those of presumed earlier origin.

THE HEAD.—Below are given particulars of how recent Deltocephalinae differ in head structure from the ancient aetalionid, *Darthula hardwickii*. Not only are the Deltocephalinae probably the most recently evolved of all cicadellids, but they are also the most widely distributed and contain the largest number of species. The characteristics of representatives of this subfamily, given below, precede those of *D. hardwickii*, which are given in parentheses. Wide maxillary plates with sensory pits, continuous with the genae (narrow maxillary plates with sensory pits, separated from the genae by a subgenal suture); hind margin of lora widely separated from the antennal bases (hind margins of lora adjacent to the antennal bases); frontoclypeus lacking any trace of epistomal suture and extending posteriorly as far as the hind margin of the face (frons separated from the postclypeus by an epistomal suture anteriorly and the arms of the epicranial suture posteriorly); ocelli situated near the sides of the frontoclypeus and close to, or on, the margin of the head separating the face from the crown (ocelli on the face of the head close to the sides of the epicranial suture and at a considerable distance from the hind margin of the face) (Evans 1975a).

THE THORAX.—Some supposed relict characters are the small pronotal paranota, such as occur in the Myerslopiini (Ulopinae), and extensions of the costal region of the tegminal pads of the nymphs of some ulopids, such as those of *Coloborrhis corticina* and also a few macropsids (Evans 1968). These paranota and the mesothorasic costal expansions are regarded as relict features because the former were possessed by many Palaeozoic insects and the latter occur also in the Psylloidea, and in some Cicadelloidea and Membracoidea, which, for other reasons, are regarded as relict forms.

THE ABDOMEN.—Among relict characters is the retention of tymbals in the nymphs as well as in the adults of some aetalionids, and the presence in the male genitalia of bisegmented subgenital plates. I have suggested that the latter, which occur in some Ulopinae, Macropsinae, and Agallinae, represent the gonocoxites and the gonostyli of the ninth abdominal segment (Evans 1975).

## CONCLUSIONS

The observations recorded in this article serve to emphasize that the factors responsible for evolutionary change are of varied nature. Some, involving major changes of structural organization, present puzzling features.

Others suggest that evolutionary developments need not always be of an adaptive nature, that isolation of populations need not always be of a geographical nature, and that the development of bizarre forms is particularly associated with isolation of populations on islands.

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# REVISION OF THE GENUS *CALLISCARTA* (HOMOPTERA: CICADELLIDAE: NEOBALINAE)[1]

Paul H. Freytag[2]

ABSTRACT.—A taxonomic revision of the Neotropical genus *Calliscarta* Stål is presented. Most of the 19 species treated are described and illustrated, including 10 that are new to science. The new species include: *abrupta* (Bolivia), *acuta* (Peru, Venezuela), *delicata* (Bolivia, Peru), *elongata* (Ecuador, Peru), *expansa* (Bolivia, Ecuador, Peru), *lora* (Peru), *marginata* (Honduras), *mexicana* (Mexico), *ornata* (French Guiana, Venezuela), *rugosa* (Venezuela). Three cases of new synonymy are proposed: *boliviana* (Osborn) (= *tinga* Kramer), *fasciata* (Osborn) [= *brunnea* (Osborn)], *decora* (Fabricius) [= *magnifica* (Osborn)].

The genus *Calliscarta* as reviewed by Linnavuori (1959) included nine species. Two species and the genus *Idiotettix* Osborn were placed in synonymy. Since then Linnavuori and Heller (1961) added one species, and Kramer (1963) added two species. In this study nine of these species are recognized as valid, three are placed in synonymy, and 10 new species are added. The limited number of specimens in collections of this genus make it a very difficult genus with which to deal. No division of this genus is made at this time even though some species groups appear to represent separate genera, such as the *fasciata* group. Much more material will be needed, especially from Central America, to know how to properly place many species. The problem of having only one sex of the majority of the species also makes it very difficult to understand relationships. For these reasons a phylogenetic study must wait until the species are better known.

## *Calliscarta* Stål

*Calliscarta* Stål 1869: 82 (type-species *Cicada decora* Fabricius); Dallas 1870: 497; Van Duzee 1890: 35; Van Duzee 1890: 79; Schulze, Kükenthal, and Heider 1927: 504; Neave 1939: 537; Evans 1947: 230; Linnavuori 1959: 27; Linnavuori and Heller 1961: 3; Metcalf 1967: 946.

*Idiotettix* Osborn 1929: 465 [type-species *Thamnotettix magnificus* Osborn (= *Cicada decora* Fabricius)]; Oman 1938: 355; Neave 1939: 763; Metcalf 1944: 161; Evans 1947: 192; Evans 1951: 9; Nast 1952: 1; Maldonado Capriles 1954: 247; Metcalf 1966: 225.

Large, robust, wedge shaped. Head wider than pronotum; crown wide, same length near eyes as median, coronal suture short; ocelli on the margin about twice their width from eyes, face elongate; postclypeus convex and long, sutures along each side starting near ocelli, with antennal ledges from postclypeus to eye. Pronotum convex, lateral margins short, posterior margin slightly but evenly emarginate. Forewing truncate, appendix well developed, with three subapical cells. Femur of hind leg with spinulation 2-2-1. Male genitalia large and mostly sclerotized. Anal tube long, cylindrical, heavily sclerotized. Pygofer always with a membranous ventral process that extends into the genital capsule, or with a long ventral process.

This genus has been previously placed in the subfamily Idiocerinae on the basis of the overall shape of the body and the large appendix. It has also been placed in the subfamily Deltocephalinae, as the ocelli are on the margin of the head near the eyes. These and other characters, plus the fact that the majority of the species are brightly colored and larger than those found in the above-mentioned subfamilies, caused Linnavuori (1959) to place this genus in the subfamily Neobalinae.

### Key to Known Males

| | | |
|---|---|---|
| 1. | Aedeagus with extra dorsal apodemal process (Figs. 56, 57); pygofer with large ventral process (Fig. 55) | *fasciata* (Osborn) |
| — | Aedeagus without extra apodemal process; pygofer with some type of apical process | 2 |
| 2(1). | Aedeagus with shaft laterally compressed, knife-shaped, and with or without small lateral processes (Figs. 10, 11, 14, 15) | 3 |

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— Aedeagus with shaft tubular (Figs. 24, 25) . . 10
3(2). Style with a lateral subapical tooth (Fig. 4) . . . 4
— Style without subapical tooth . . . . . . . . . . . . . . 5
4(3). Pygofer truncate with a small apical process (Fig. 1) . . . . . . . . . . . . . . . . . . *decora* (Fabricius)
— Pygofer gradually narrowing to bluntly pointed apex, median of ventral margin with two small teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tartessoides* Linnavuori & Heller
5(3). Pygofer with apical process bifurcate (Figs. 13, 17, 18) . . . . . . . . . . . . . . . . *boliviana* (Osborn)
— Pygofer with apical process not bifurcate (Fig. 19) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6. Pygofer with apical process dorsally produced and pointed (Fig. 5) . . . . . . . . . . . . . . . . . . . . . . 7
— Pygofer with apical process bird-head-shaped (Fig. 9) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
7. Style thickened to near apex (Fig. 8); aedeagus with small lateral processes (Figs. 6, 7) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *elongata*, n. sp.
— Style narrowing to pointed apex (Fig. 46); aedeagus with conspicuous processes (Figs. 44, 45) . . . . . . . . . . . . . . . . . . . . . . *delicata*, n. sp.
8. Aedeagus with conspicuous processes (Figs. 48, 49) . . . . . . . . . . . . . . . . . . . . . . *ornata*, n. sp.
— Aedeagus without processes (Figs. 10, 11) . . . 9
9. Style long and abruptly curved subapically (Fig. 12) . . . . . . . . . . . . . . . . . . . . . *invita* (Nast)
— Style short and evenly curved near apex (Fig. 22) . . . . . . . . . . . . . . . . . . . . . . . . . . *lora*, n. sp.
10(2). Style foot-shaped at apex (Fig. 26) . . . . . . . . . 11
— Style pointed at apex (Fig. 42) . . . . . . . . . . . . 13
11(10). Aedeagus with shaft expanded at apex (Fig. 32) . . . . . . . . . . . . . . . . . . . . . . . . *abrupta*, n. sp.
— Aedeagus with shaft not expanded at apex . . 12
12(11). Aedeagus with small apical processes (Fig. 24) . . . . . . . . . . . . . . . . . . . . . . . . . . *magna* (Osborn)
— Aedeagus with larger subapical processes (Fig. 28) . . . . . . . . . . . . . . . . . . . *expanda*, n. sp.
13(10). Aedeagus with processes expanded at base (Fig. 40) . . . . . . . . . . . . . . . . . *columbiana* (Nast)
— Aedeagus with thin, spinelike processes (Fig. 36) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
14(13). Aedeagus with gonopore basal to processes (Fig. 37) . . . . . . . . . . . . . . . . . . . . *stigmata* (Nast)
— Aedeagus with gonopore apical to processes (Fig. 53) . . . . . . . . . . . . . . . . . . *corvenda* Kramer

Key to Known Females

1. Pronotum longitudinally banded . . . . . . . . . . . 2
— Pronotum not so marked . . . . . . . . . . . . . . . . . 3
2(1). Seventh sternum unusually long, over twice length of sixth (Fig. 61) . . . . . . *fasciata* (Osborn)
— Seventh sternum shorter, about twice or less length of sixth (Fig. 65) . . . . . . . *mexicana*, n. sp.
3(1). Seventh sternum truncate, with a median emargination . . . . . . . . . . . . . . . . . *rugosa*, n. sp.
— Seventh sternum not truncate, posterior margin usually rounded . . . . . . . . . . . . . . . . . . . . . . 4
4(3). Head with a frontal margin, bright yellow and black . . . . . . . . . . . . . . . . . . . . . *marginata*, n. sp.
— Head rounded to face . . . . . . . . . . . . . . . . . . . 5
5(4). Ovipositor short, less than 2 mm in length (Fig. 63) . . . . . . . . . . . . . . . . . . . . . *acuta*, n. sp.
— Ovipositor long, more than 2 mm in length (Fig. 62) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6(5). Seventh sternum with median emargination of posterior margin V-shaped (Fig. 59) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ornata*, n. sp.
— Seventh sternum with median emargination of posterior margin U-shaped (as in Fig. 62) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *decora* (Fabricius)

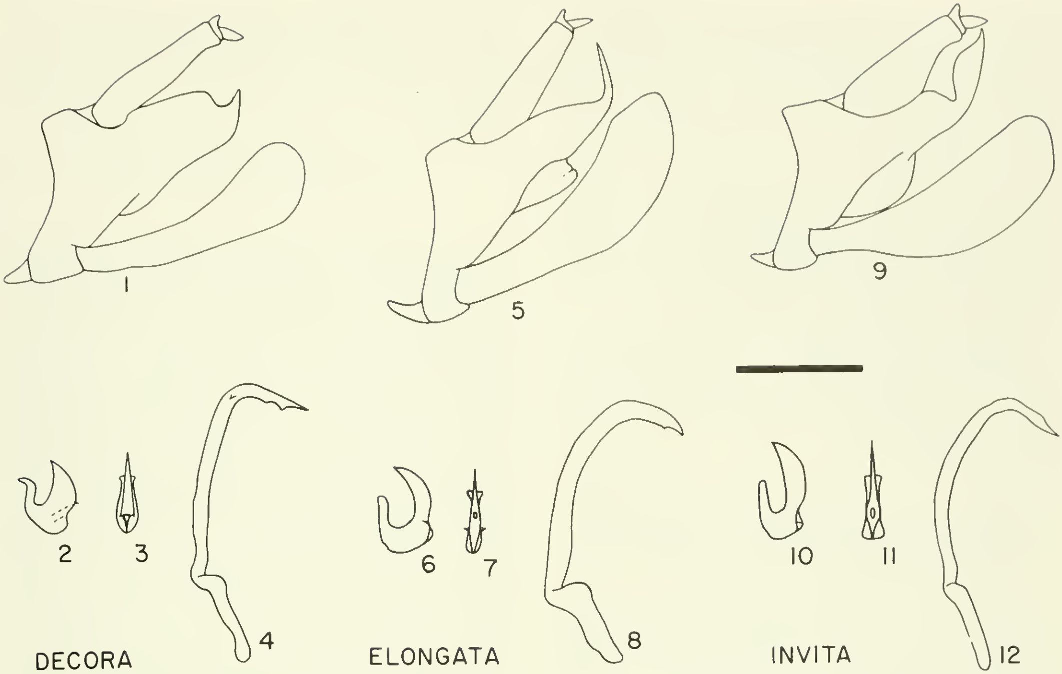
The *decora* species group is characterized by having orange transverse bands on the head, and the aedeagus laterally flattened and knife-shaped. The following seven species are placed in this group.

## *Calliscarta decora* (Fabricius)

Figs. 1–4, 66

*Cicada decora* Fabricius 1803: 69. (South America, possibly from Brazil; Stockholm Museum).
*Tettigonia decora:* Signoret 1853: 327; Walker 1858: 200; Dohrn 1859: 88.
*Calliscarta decora:* Stål 1869: 83; Dallas 1870: 495; Distant 1908: 524; Evans 1947: 230; Linnavuori 1959: 29; Metcalf 1967: 946.
*Thamnotettix magnificus* Osborn 1924: 424. (Cuatro Ojos, Santa Cruz, Bolivia; Carnegie Museum). *New synonymy*
*Idiotettix magnificus:* Osborn 1929: 465; Oman 1938: 395; Evans 1947: 192; Nast 1952: 1; Maldonado Capriles 1954: 250; Metcalf 1966: 227.
*Calliscarta magnifica:* Linnavuori 1959: 28.
*Idiotettix festivus* Maldonado Capriles 1954: 248. (Cunucunuma River, F. T. Amazonas, Venezuela; U.S. National Museum).

Length of males 9.5-11.5 mm.; female 12 mm. Head reddish yellow above antennal sockets, yellow below, with three orange transverse bands, one just above and one just below ocelli and the other above base of antennae. Pronotum reddish yellow with two darker red transverse bands, one along anterior margin and one across middle, and one yellowish green band along posterior margin continuing to anterior of lateral margins near eyes. Scutellum reddish brown. Forewing generally dark reddish brown, claval area lighter brown with four large, yellowish green spots, costal margin red, and a row of six to eight large, yellowish green spots through middle of wing from base to appendix, apex




Figs. 1–4. *Calliscarta decora* (Fabricius), from Peru; 1, lateral view of male genital segments; 2, lateral view of aedeagus; 3, ventral view of aedeagus; 4, ventrolateral view of style.

Figs. 5–8. *Calliscarta elongata*, n. sp., holotype: 5, lateral view of male genital segments; 6, lateral view of aedeagus; 7, ventral view of aedeagus; 8, ventrolateral view of style.

Figs. 9–12. *Calliscarta invita* (Nast), from Ecuador: 9, lateral view of male genital segments; 10, lateral view of aedeagus; 11, ventral view of aedeagus; 12, ventrolateral view of style. All drawn to the same scale; the line equals 1 mm.

smoky brown. Ventral surface entirely yellow.

MALE GENITALIA.—Pygofer truncate with a short, apical, spinelike process (Fig. 1). Genital plates large, roundedly expanded at apex (Fig. 1). Style long, bent at right angle three-quarters of distance from base, apex pointed with a subapical tooth on inner margin, and a small but distinct spine at the bend (Fig. 4). Aedeagus short, laterally flattened, broad in lateral view, apex pointed, with a pair of small processes on caudal margin near gonopore (Figs. 2, 3).

FEMALE GENITALIA.—Seventh sternum large, twice length of sixth, with a shallow, median, U-shaped emargination similar to *ornata*.

TYPE.—Holotype male of *decora* not seen, but illustrated by Linnavuori (1959). Type is from South America, and Dohrn (1859) gave Brazil as the possible type locality.

DISTRIBUTION.—Known are specimens from: BOLIVIA: one female, Cuatro Ojos, November 1913, Steinbach Coll., (holotype of *magnificus*) Carnegie Museum. BRAZIL: one male, ? (holotype of *decora*) Stockholm Museum. ECUADOR: one male, Pompeya, 13–25 May 1965, Luis E. Peña Coll., Ramos Collection; one male, Coca, May 1965, Luis E. Peña Coll., Ramos Collection; two males, Napo, Prov. Limoncocha, 10 June 1977, Dave L. Vincent Coll., U.S. National Museum. FRENCH GUYANA: one male, Cabret République, 29 August 1975, Guyane Française Mission M. Boulard, et P. Pompanon Coll., Muséum Paris. GUYANA: one male, Bartica, 20–30 March 1901, H. S. Parish Coll., (allotype of *magnificus*) Ohio State University Collection. PERU: four males, Avispas, October 1962, Luis E. Peña Coll., Ramos Collection. VENEZUELA: one male, Cunucunuma River, F. T. Amazonas, 28 April 1950, J. Maldonado Capriles Coll. (holotype of *festivus*) U.S. National Museum; one male, Anacoco, Bolivar, 60 M, 6°5′N:61°8′W, 10–30 August 1979, Expedicion La Salle, University of Central Venezuela Collection.

NOTES.—This species appears to be widely

distributed in South America but is poorly represented in collections. Much confusion concerning the identification of this species has occurred because the color pattern is not fully developed in some specimens. However, this species can be quickly recognized by the small spine on the male style, which is found on only one other known species, *tartessoides*. For now the female must be recognized by the color pattern, which is the same as in the male.

The types of *magnificus* and *festivus* were examined and found to represent the same species. Linnavuori (1959) synonymized *festivus* with *decora*.

### *Calliscarta tartessoides* Linnavuori & Heller

*Calliscarta tartessoides* Linnavuori & Heller 1961: 3. (Hacienda Mascoitania, Peru; Staatlichen Museum für Naturkunde, Stuttgart).

This species was illustrated when described, and no additional information can be added at this time. It appears to be closely related to *decora*.

Length of male 9.5 mm; female unknown. Brownish yellow. Head light yellow, with a reddish orange transverse band across vertex between eyes; face with an orange transverse band between ocelli and another across middle of face, and a dark brown spot underneath each ocellus. Pronotum with anterior margin light yellow, posterior two-thirds darker marbled with darker orange. Scutellum faintly dark orange. Forewing mostly translucent, with veins brown; costal vein darker brown in middle. Ventral surface light yellow with some yellow-orange and brown markings on legs and abdomen.

MALE GENITALIA.—Pygofer narrowing to a posteriorly projecting, bluntly pointed apex, with two small spines on ventral margin near middle. Genital plates large and truncate at apex. Style long, bent laterally on apical fourth, apex pointed, a small subapical tooth on inner margin. Aedeagus laterally flattened, knife-shaped, without noticeable processes, gonopore on ventral margin near middle of shaft.

TYPE.—Holotype (male), PERU, Hacienda Mascoitania, 10–12 November 1957, Urwald Coll., Staatlichen Museum für Naturkunde, Stuttgart.

NOTES.—This species is known only from the type specimen, which I have not seen. It is a species like *decora*, with a tooth on the style, but a color pattern that is more like *magna*. More material is needed to properly place this species.

### *Calliscarta elongata*, n. sp.

Figs. 5–8

This species resembles *decora* in general appearance, but with different male genitalia.

Length of males 10–10.1 mm; female unknown. Head creamy yellow, crown having a red-violet tinge, with four orange transverse bands, one across middle of crown between eyes, one just below ocelli, two fainter bands across postclypeus; a black band on each side from base of antenna to anteclypeus along side of postclypeus. Pronotum orange, with a band along posterior margin and two central spots greenish yellow. Scutellum orange with a small yellow spot in middle of each lateral margin. Forewing orange anteriorly, fading to brown posteriorly, median of costal vein with a reddish tinge, four greenish yellow spots on clavus, three at base and one near middle, four yellow spots on corium, apical cells smoky brown with an L-shaped translucent spot pattern. Ventral surface generally creamy yellow, fore tibiae and tarsi brownish yellow.

MALE GENITALIA.—Pygofer narrowing to apex, apex a dorsally projecting, pointed process (Fig. 5). Genital plate enlarged and expanded on apical half, apex bluntly rounded (Fig. 5). Style stout, uniform width throughout, hooked apically, apex with a very small subapical tooth (Fig. 8). Aedeagus laterally flattened, knife-shaped, gonopore medially on ventral margin, a pair of small lateral processes basal to gonopore (Figs. 6, 7).

TYPE.—Holotype (male), ECUADOR, Napo, Lago Agrio (18 km E), 28 August 1975, Río Aguarico, collected on gravel bar at blacklight, Langley, Cohen, Cantor, Yingling Coll., Ecuador–Peace Corps–Smithsonian Institution Aquatic Insect Survey, in the U.S. National Museum. Paratypes: ECUADOR, one male, same data as holotype, except 23 September 1975 and Andrea Langley Coll., University of Kentucky Collection; one male, same data as holotype, except 19 September 1975 and Andrea Langley Coll., U.S. National Museum; PERU, Avispas, October 1962, Luis E. Peña Coll., Ramos Collection.

## *Calliscarta invita* (Nast)

Figs. 9–12

*Idiotettix invitus* Nast 1952: 3. (Santa Inez, Ecuador, Polish Museum of Zoology); Maldonado Capriles 1954: 250; Metcalf 1966: 226.

*Calliscarta invita:* Linnavuori 1959: 30; Linnavuori and Heller 1961: 3.

Length of males 10–10.6 mm; female unknown. Head brownish yellow, with a tinge of violet on crown and postclypeus; an orange transverse band across middle of crown between eyes, another orange transverse band below ocelli, two brownish orange transverse bands on postclypeus, a black band on each side from base of antennae to anteclypeus along sides of postclypeus. Pronotum mostly orange brown, lateral margins yellow. Scutellum light brown. Forewing light brown, with veins and obscure spots darker brown, median of costa reddish orange, small, white, translucent spots on clavus and corium; apical area smoky brown with three translucent spots. Ventral surface mostly brownish yellow, brown spot on propleura and sterna, fore legs with most of tibiae and entire tarsi brown, middle legs with base and apex of tibiae and entire tarsi brown.

MALE GENITALIA.—Pygofer truncately narrowed to apex, which is projected slightly dorsad in the shape of a bird's head (Fig. 9). Genital plate large, expanded in lateral view, truncate (Fig. 9). Style elongate, even width throughout, hooked apically, with a pointed apex (Fig. 12). Aedeagus laterally flattened, knife-shaped, without processes, gonopore on ventral margin near base of shaft (Figs. 10, 11).

TYPE.—Holotype (male), ECUADOR, Santa Inéz, R. Haensch Coll., Polish Museum of Zoology.

DISTRIBUTION.—Five males are known for this species. Linnavuori and Heller (1961) reported two males from PERU, Hacienda Mascoitania, 10–12 September 1957, Urwald Coll., Staatlichen Museum für Naturkunde, Stuttgart. I have seen two males from ECUADOR, Río Margajita, Río Pastaza, 1250 m, 20 March 1939, F. M. and H. H. Brown Coll., University of Kansas Collection.

## *Calliscarta boliviana* (Osborn)

Figs. 13–18

*Idiotettix bolivianus* Osborn 1929: 466. (Coroico, La Paz, Bolivia, Ohio State University Collection); Oman 1938: 395; Nast 1952: 1; Maldonado Capriles 1954: 250; Metcalf 1966: 225.

*Calliscarta boliviana:* Linnavuori 1959: 29.

*Calliscarta tinga* Kramer 1963: 205. (Tingo María, Huanuco, Peru, U.S. National Museum). *New synonymy*

Length of males 9.1–10 mm; female unknown. General color as in *invita,* pronotum with a band of yellow along posterior margin and lateral margins and white, translucent spots on forewings less conspicuous.

MALE GENITALIA.—Pygofer quite variable, narrowing to near apex, which projects dorsad in some type of bifurcate process (Figs. 13, 17, 18). Genital plates greatly expanded on apical half (Fig. 13). Style elongate, narrowing slightly to apex, hooked apically, apex with a ventral subapical tooth (Fig. 16). Aedeagus laterally flattened, knife-shaped, gonopore on ventral margin near base of shaft, with a small pair of laterally projecting processes basal to gonopore (Figs. 14, 15).

TYPE.—Holotype (male), BOLIVIA, Coroico, Ohio State University Collection.

DISTRIBUTION.—This species is known from 10 male specimens. Besides the two types, I have seen: BOLIVIA, one male, Cristal Mayn, Chapare, 28 August 1949, L. E. Peña Coll., University of Kansas Collection; PERU, four males, Avispas, September 1962, Luis E. Peña Coll.; two males, Quincemil, August 1962, Luis E. Peña Coll., Ramos Collection, and one from each locality in University of Kentucky Collection; PANAMA, El Volcán de Chiriqui, 26 February 1936, W. J. Gertsch Coll., American Museum of Natural History.

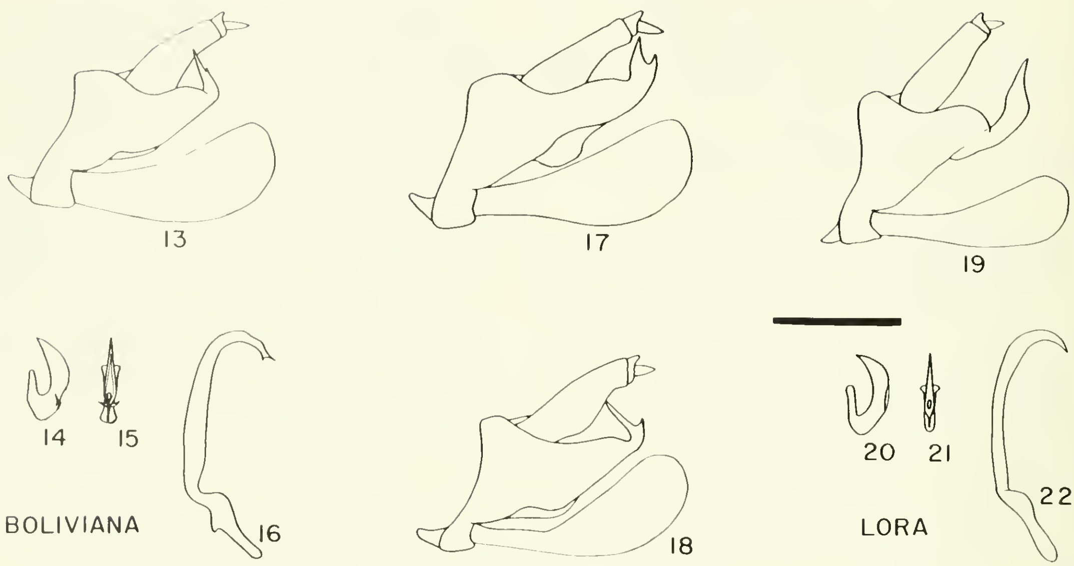
NOTES.—This species is quite variable in the shape of the apex of the pygofer, but it is the only species of the genus with the apex bifurcate. No two specimens seen have the same shape, and I consider this to be just a variation at this time; however, this may prove to be a complex of very closely related species.

## *Calliscarta lora*, n. sp.

Figs. 19–22

This species resembles *invita* in general appearance, but with distinct male genitalia.

Length of male 9.3–9.9 mm; female unknown. Head, pronotum, and scutellum as in *elongata.* Forewing with clavus mostly orange, with three yellow spots, two transverse spots anteriorly, one longitudinal spot along posterior part of claval suture; corium brown,




Figs. 13–16. *Calliscarta boliviana* (Osborn), holotype: 13, lateral view of male genital segments; 14, lateral view of aedeagus; 15, ventral view of aedeagus; 16, ventrolateral view of style.

Figs. 17–18. Lateral views of male genital segments of other specimens of *C. boliviana* from Bolivia.

Figs. 19–22. *Calliscarta lora*, n. sp., holotype: 19, lateral view of male genital segments; 20, lateral view of aedeagus; 21, ventral view of aedeagus; 22, ventrolateral view of style. All drawn to the same scale; the line equals 1 mm.

median of costal vein with a reddish tinge, with four yellow spots, two at base, one (sometimes two) above reddish tinge of costa, and one a continuation of longitudinal spot on clavus; apical cells smoky brown, with three small, translucent spots. Ventral surface creamy yellow, fore tibiae and tarsi brownish yellow.

MALE GENITALIA.—Pygofer narrowing to apex that extends as a large bird's-head-shaped process (Fig. 19). Genital plate gradually expanding to a large, truncate apex (Fig. 19). Style elongate, hooked apically, with a pointed apex (Fig. 22). Aedeagus laterally flattened, knife-shaped, gonopore on ventral margin near middle, without processes (Figs. 20, 21).

TYPE.—Holotype (male), PERU, Quincemil, August 1962, Luis E. Peña Coll., in the Ramos Collection but will be deposited in U.S. National Museum through courtesy of Dr. Ramos. Paratypes: PERU, two males, same data as holotype; one male, Quincemil, October 1962, Luis E. Peña Coll.; two males, Avispas, September 1962, Luis E. Peña Coll., three in the Ramos Collection and two in the University of Kentucky Collection.

NOTES.—This species has a distinct color pattern and male genitalia that make it possible to separate it from other known species that also occur in Peru.

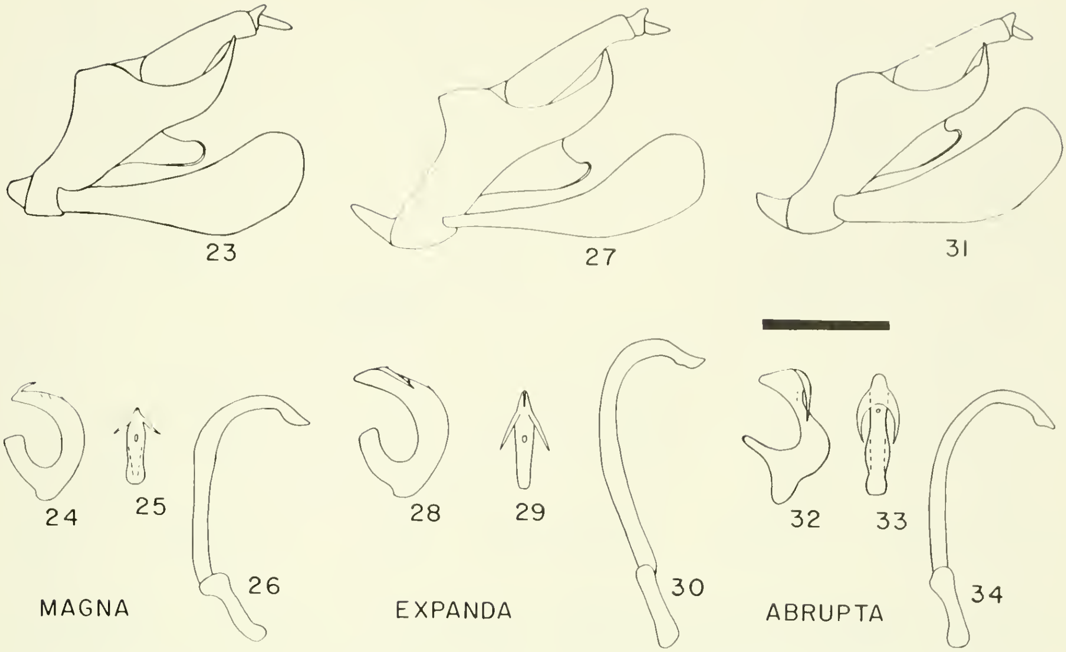
### *Calliscarta delicata*, n. sp.

Figs. 43–46

This species resembles *invita* in general appearance, but with distinct male genitalia.

Length of male 8.5–10.1 mm; female unknown. Head yellow, with four orange transverse bands, one above ocelli, one below ocelli, one between antennae and one along lower margin of postclypeus. Pronotum orange, with green posterior margin extending along lateral margins and a green transverse band in anterior half. Scutellum mostly orange. Forewing generally smoky brown, with claval suture, anterior third of costa, and small spots at ends of claval veins green; costa red near middle; corium with two orange bands extending from near base to apical veins, one along claval suture, other along costa; apical cells smoky brown with three transverse, opaque spots. Abdominal segments orange.

MALE GENITALIA.—Pygofer narrowing to somewhat expanded apex, with a dorsally projecting, apical, pointed process (Fig. 43). Genital plate gradually expanded to a large, truncate apex (Fig. 43). Style narrowing and




Figs. 23–26. *Calliscarta magna* (Osborn), from Brazil: 23, lateral view of male genital segments; 24, lateral view of aedeagus; 25, ventral view of aedeagus; 26, ventrolateral view of style.

Figs. 27–30. *Calliscarta expanda*, n. sp., holotype: 27, lateral view of male genital segments; 28, lateral view of aedeagus; 29, ventral view of aedeagus; 30, ventrolateral view of style.

Figs. 31–34. *Calliscarta abrupta*, n. sp., holotype: 31, lateral view of male genital segments; 32, lateral view of aedeagus; 33, ventral view of aedeagus; 34, ventrolateral view of style. All drawn to the same scale; the line equals 1 mm.

curving laterally near pointed apex (Fig. 46). Aedeagus laterally compressed with a pair of long, curved processes from base of shaft, gonopore medially on ventral margin, apex bluntly pointed (Figs. 44, 45).

TYPE.—Holotype (male), PERU, Tingo María, 20 June 1982, Fisk, Ohio State University Collection. Paratypes: two males, same data as holotype, one in Ohio State University Collection and one in University of Kentucky Collection. Two males, BOLIVIA, El Palmar, Cochabamba, Chaparé, 8–15 September 1955, Luis E. Peña Coll., Ramos Collection.

NOTES.—This species can be separated from *invita* by the longer processes on the aedeagus.

The *ornata* species group is characterized by a single, transverse, black band on the face that replaces the orange transverse bands of the *decora* group, and by an aedeagus that is flattened and knife-shaped. Only one species, *ornata*, is placed here.

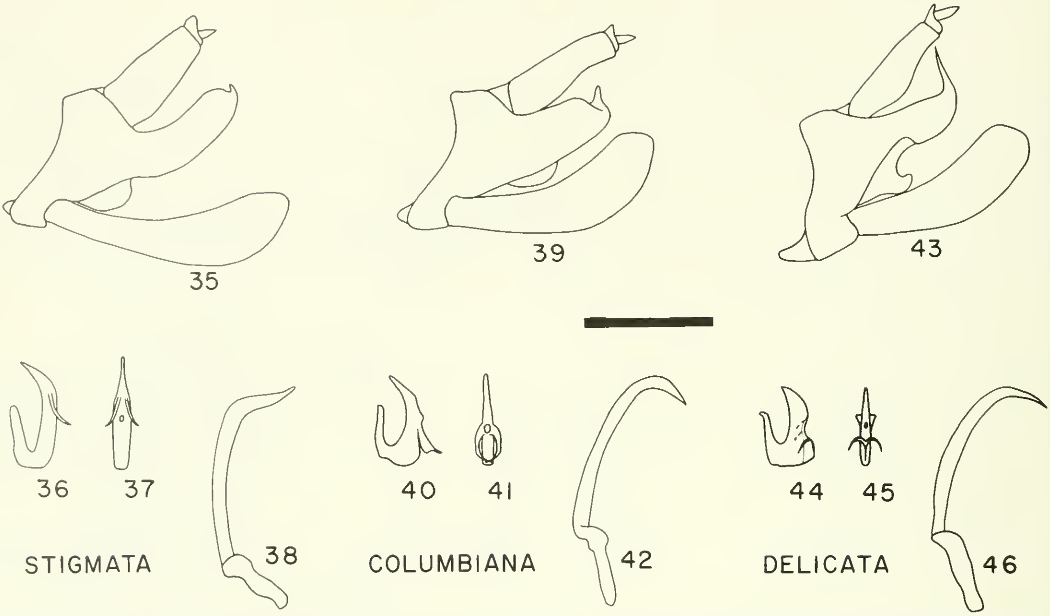
### *Calliscarta ornata*, n. sp.

Figs. 47–50, 59, 67

This species resembles *invita* in general appearance, but with unique black band on face instead of usual orange bands.

Length of male 9.4–10.1 mm; female 10–11 mm. Head creamy yellow with a reddish tinge; an irregular, black, transverse band below ocelli, a large, black spot in middle of postclypeus, a black, V-shaped band from antennal bases along sides of postclypeus over entire anteclypeus. Pronotum creamy yellow, with a large, irregular, transverse, brown band across middle, posterior margined with greenish yellow. Scutellum mostly creamy yellow. Forewing brown, with many large, greenish yellow spots, apical cells smoky brown, with two large, translucent spots.

MALE GENITALIA.—Pygofer narrowed to a truncate apex, with a large, nearly bird's-head-shaped apical process (Fig. 47). Genital plate large, greatly expanded at apex, which is bluntly rounded (Fig. 47). Style elongate,




Figs. 35–38. *Calliscarta stigmata* (Nast), from Colombia: 35, lateral view of male genital segments; 36, lateral view of aedeagus; 37, ventral view of aedeagus; 38, ventrolateral view of style.

Figs. 39–42. *Calliscarta columbiana* (Nast), from Colombia: 39, lateral view of male genital segments; 40, lateral view of aedeagus; 41, ventral view of aedeagus; 42. ventrolateral view of style.

Figs. 43–46. *Calliscarta delicata*, n. sp., holotype: 43, lateral view of male genital segments; 44, lateral view of aedeagus; 45, ventral view of aedeagus; 46, ventrolateral view of style. All drawn to the same scale; the line equals 1 mm.

hooked apically, with a pointed apex (Fig. 50). Aedeagus laterally flattened, knife-shaped, with a pair of recurved processes on ventral margin near base of shaft, gonopore on ventral margin just apical to bases of processes (Figs. 48, 49).

FEMALE GENITALIA.—Seventh sternum enlarged, rounded posterior margin with a large, median, V-shaped emargination (Fig. 59). Ovipositor extending twice its width beyond pygofer. Pygofer narrowing to apex in ventral view.

TYPE.—Holotype (male), FRENCH GUYANA, Saint-Elie, 30 August–2 September 1975, Guyane Française Mission, M. Boulard et P. Pompanon Coll., Paris Museum. Allotype (female), same data as holotype. Paratypes: FRENCH GUYANA, one female, Carbet Lavaud (Rive Surinamienne), 24–26 September 1975, Itani (Guyanes) Mission, M. Boulard, P. Jauffret et P. Pompanon Coll.; one female, Em Gouchure de la Crique Oyaricoulet, 23 September 1975, Itani (Guyanes) Mission, M. Boulard, P. Jauffret et P. Pompanon Coll.; one female, Alicoto-Oyapock-Guyane, 13 November 1969, Piège lumineux, Guyane Mission, Balachowsky, Gruner Coll., Oct.–Nov. 1969, Paris Museum; BRAZIL, one female, Chapada, September, C. F. Baker Coll.; one female, Chapada, October, C. F. Baker Coll., U.S. National Museum; VENEZUELA, one male, San Carlos de Río Negro, T. F. Amazonas, 7–13 September 1982, A. Chacòn, G. Yepez Gil Coll.; one female, Sta. Lucía, T. F. Amazonas, 15–21 September 1982, A. Chacòn, G. Yepez Gil Coll.; one male, one female, Río Surukum, Carretera Sta., Elena Icabaru, Bolivar, 850 m, 19–31 January 1985, F. Fernandez Y., Anibal Chacòn, Jurg Demarmels Coll., University of Central Venezuela Collection.

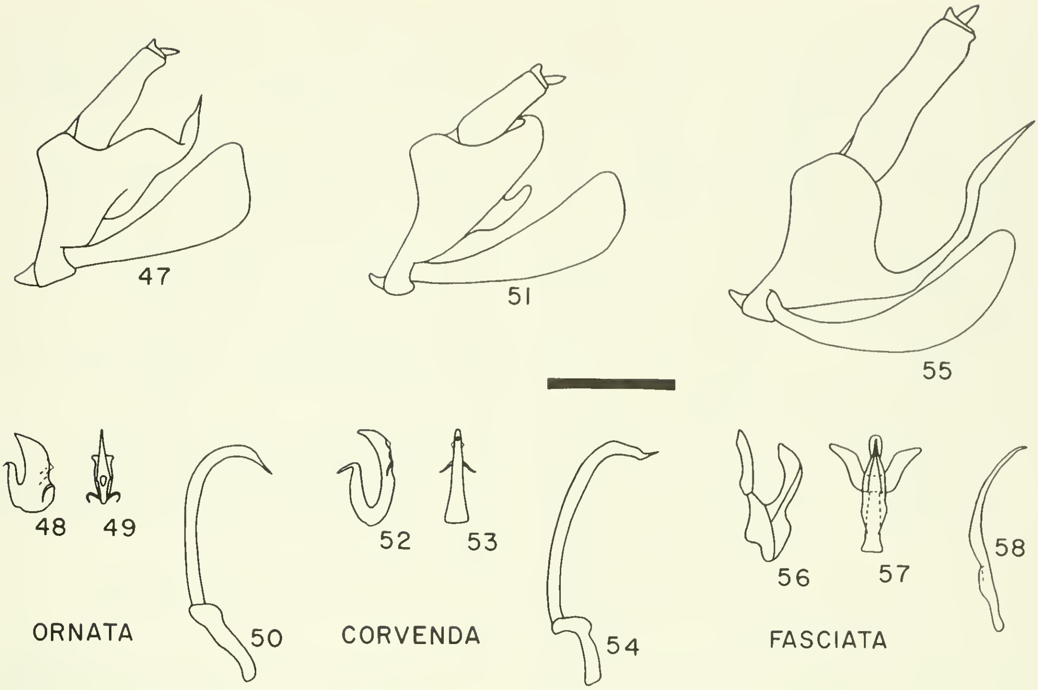
NOTES.—This species can be easily separated from the known species of this genus on the basis of the dark band across the face.

The *magna* species group is characterized by having the head mottled with brown and the aedeagal shaft tubular with apical or subapical processes. The following three species are placed in this group.

### *Calliscarta magna*, (Osborn)

Figs. 23–26

*Idiocerus magnus* Osborn 1923: 13. (San Antonio de Guapore, MattoGrosso, Brazil, Carnegie Museum).




Figs. 47–50. *Calliscarta ornata*, n. sp., holotype: 47, lateral view of male genital segments; 48, lateral view of aedeagus; 49, ventral view of aedeagus; 50, ventrolateral view of style.

Figs. 51–54. *Calliscarta corvenda* Kramer, from Venezuela: 51, lateral view of male genital segments; 52, lateral view of aedeagus; 53, ventral view of aedeagus; 54, ventrolateral view of style.

Figs. 55–58. *Calliscarta fasciata* (Osborn), from Brazil: 55, lateral view of male genital segments; 56, lateral view of aedeagus with connector to anal tube; 57, ventral view of aedeagus and connector to anal tube; 58, ventrolateral view of style. All drawn to the same scale; the line equals 1 mm.

*Idiotettix magnus:* Maldonado Capriles 1954: 247; Metcalf 1966: 227.
*Calliscarta magna:* Linnavuori 1959: 30.

Length of male 9–10 mm; female unknown. Head, pronotum, and scutellum creamy yellow with a reddish violet tinge, greatly mottled with brown. Forewing mostly translucent, veins dark brown; clavus with a large, fuscous spot at middle and apex; apical cells smoky brown, with two transverse, translucent spots. Ventral surface mostly creamy yellow, with fore and middle legs with apex of tibiae and entire tarsi brownish yellow.

MALE GENITALIA.—Pygofer gradually narrowing to a pointed apex (Fig. 23). Genital plate large, greatly expanded on apical half (Fig. 23). Style elongate, hooked apically, apex bluntly pointed (Fig. 26). Aedeagus tubular, with pair of small, lateral, apical processes, gonopore subapical on ventral margin (Figs. 24, 25).

TYPE.—Holotype (male), BRAZIL, Rondônia, Santo Antonio de Guaporé (Río Guaporé), 26 July 1909, Haseman Coll., Carnegie Museum.

DISTRIBUTION.—Known only from Brazil on the basis of the type and the following specimens: BRAZIL, five males, São Félice, Camp IV, Moyen Xingu, (Brèsil) Mission, M. Boulard, P. Jauffret et P. Pompanon Coll., four in Muséum Paris and one in University of Kentucky Collection.

### *Calliscarta expanda*, n. sp.

Figs. 27–30

This species resembles *magna* in general appearance, but with distinct male genitalia.

Length of male 9.7–10.5 mm.; female unknown. Head, pronotum, and scutellum creamy violet, mottled with brown. Forewing brown, with most cells translucent, veins dark brown; apical cells smoky brown, with three or four large, translucent, transverse spots. Ventral surface creamy yellow heavily marked with brown.

MALE GENITALIA.—Pygofer narrowing to a

pointed apex (Fig. 27). Genital plate large, expanded on apical half (Fig. 27). Style elongate, hooked apically, with apex bluntly pointed, notched subapically (Fig. 30). Aedeagus tubular, with subapical, large, lateral pair of processes, gonopore on ventral margin subapical to processes (Figs. 28, 29).

TYPE.—Holotype (male), ECUADOR, Napo, Lago Agrio, 19 September 1975, at blacklight, Andrea Langley Coll., Ecuador–Peace Corps–Smithsonian Institution Aquatic Insect Survey, U.S. National Museum. Paratypes: ECUADOR, one male, same data as holotype, except 23 September 1975, (18 km E) Río Aguarico; two males, same data, except 28 August 1975, collected on gravel bar, Langley, Cohen, Cantor, Yingling Coll., U.S. National Museum; PERU, one male, Loreto, Ucayali R., Yarina Cocha, 24 September 1953, Peter Hocking Coll., Field Museum; one male, Quincemil, August 1962, Luis E. Peña Coll.; one male, Loromavo, September 1962, Luis E. Peña Coll., Ramos Collection; BOLIVIA, Rurrenbaque, 10–23 October 1956, Luis E. Peña Coll., Ramos Collection.

NOTES.—This species is similar to *magna*, but the aedeagus is larger and with longer, more subapical processes.

### *Calliscarta abrupta*, n. sp.
Figs. 31–34

This species is related to *magna*, but with a distinctly different aedeagus.

Length of male 9.8 mm; female unknown. Head, pronotum, and scutellum mostly yellow tinted with red. Head with a small, brown spot behind each ocellus next to eye, another larger, brown spot below each ocellus next to eye. Postclypeus with brown dashes on each side and brown speckles over remainder of surface. Pronotum speckled with brown. Forewings mostly brown, claval area with opaque spots at ends of claval veins, costal vein yellow, two cell rows behind costal vein transparent, giving wing appearance of having a brown longitudinal band through middle, apical cells smoky brown with several large, opaque spots.

MALE GENITALIA.—Pygofer narrowing gradually to an upturned, pointed apex (Fig. 31). Genital plate enlarged on apical half, truncate (Fig. 31). Style nearly same width to apex, hooked apically, with apex foot-shaped (Fig. 34). Aedeagus tubular, with shaft bent at right angle near middle, apex expanded with a pair of subapical large processes extending along sides of shaft halfway to base, gonopore on ventral margin just basal to processes (Figs. 32, 33).

TYPE.—Holotype (male), BOLIVIA, Rurrenabaque, 10–23 October 1956, Luis E. Peña Coll., in Ramos Collection but is being deposited in U.S. National Museum through courtesy of Dr. Ramos.

NOTES.—This species can be separated from the other species of the genus by the distinct aedeagus.

The *stigmata* species group is characterized by having the head mottled with brown, and the aedeagal shaft tubular with processes near middle. The following four species are placed in this group.

### *Calliscarta stigmata* (Nast)
Figs. 35–38

*Idiotettix stigmatus* Nast 1952: 2. (Hac. Pehlke [probably Magdalena], Colombia, Polish Museum of Zoology); Maldonado Capriles 1954: 250; Metcalf 1966: 227.

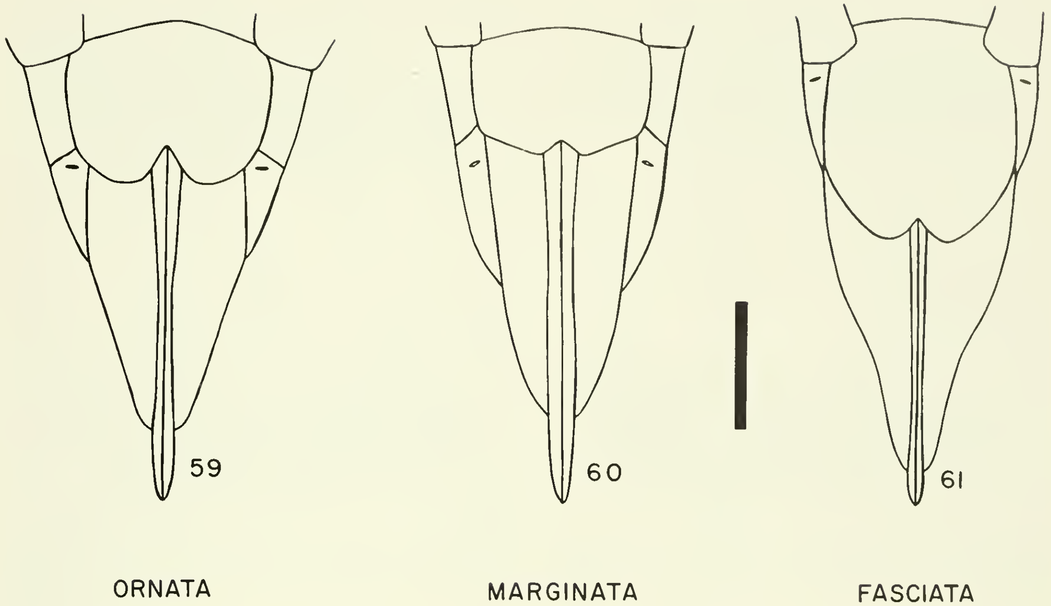
*Calliscarta stigmata:* Linnavuori 1959: 31.

Length of male 8.5–9.4 mm; female unknown. Head, pronotum, and scutellum grayish yellow tinged with violet, mottled with brown; orange bands of crown and face obscure. Forewing brown, with numerous whitish, translucent spots. Ventral surface brownish yellow; legs banded with brown.

MALE GENITALIA.—Pygofer narrowing to a long, tubular, apical area, apex with small, dorsally projecting process (Fig 35). Genital plate long, expended on apical half, bluntly rounded at apex (Fig. 35). Style long, bent apically, with pointed apex (Fig. 38). Aedeagus tubular, shaft elongate, apex bent dorsad and pointed, a pair of lateral processes at base of apical bend, gonopore basal to processes on ventral margin (Figs. 36, 37).

TYPE.—Holotype (male), COLOMBIA, Hacienda Pehlke, 1925, Pehlke Coll., Polish Museum of Zoology.

DISTRIBUTION.—This species is known from eight male specimens. The holotype and five paratypes are from Colombia and are in the Polish Museum of Zoology, and I have seen one male, COLOMBIA, Alban, Cund., 10 September 1965, J. A. Ramos Coll., Ramos Collection; and one male, VENEZUELA, Río Frío,




Figs. 59–61. *Calliscarta* spp., ventral view of female segments: 59, *C. ornata*, n. sp., allotype; 60, *C. marginata*, n. sp., holotype; 61, *C. fasciata* (Osborn), from Brazil. All drawn to the same scale; the line equals 1 mm.

Tachira, 600 m, 11–14 December 1980, J. A. Clavijo, A. Chacn, J. Ayala Coll., University of Central Venezuela Collection.

### *Calliscarta columbiana* (Nast)
Figs. 39–42

*Idiotettix columbianus* Nast 1952: 2. (Hac. Pehlke [probably Magdalena], Colombia, Polish Museum of Zoology); Maldonado Capriles 1954: 250; Metcalf 1966: 226.
*Calliscarta columbiana:* Linnavuori 1959: 29.

Length of male 8–9.1 mm; female unknown. General color pattern as in *stigmata*, except lighter in color and legs only faintly banded with brown.

MALE GENITALIA.—Pygofer narrowing to truncate apex with a small, dorsad projecting process (Fig. 39). Genital plates large, expanded, truncate at apex (Fig. 39). Style elongate, hooked apically, with pointed apex (Fig. 42). Aedeagus semitubular, apex bluntly pointed, with a pair of basally expanded, lateral processes halfway to base, gonopore on ventral margin at base of processes (Figs. 40, 41).

TYPE.—Holotype (male), COLOMBIA, Hacienda Pehlke, 1921, Pehlke Coll., Polish Museum of Zoology.

DISTRIBUTION.—This species is known only from Colombia from eight male specimens. The holotype and six paratypes are in the Polish Museum of Zoology, and I have seen one male, Alto Río Opon, Santander, January 1950, L. Richter Coll., Ramos Collection.

### *Calliscarta corvenda* Kramer
Figs. 51–54

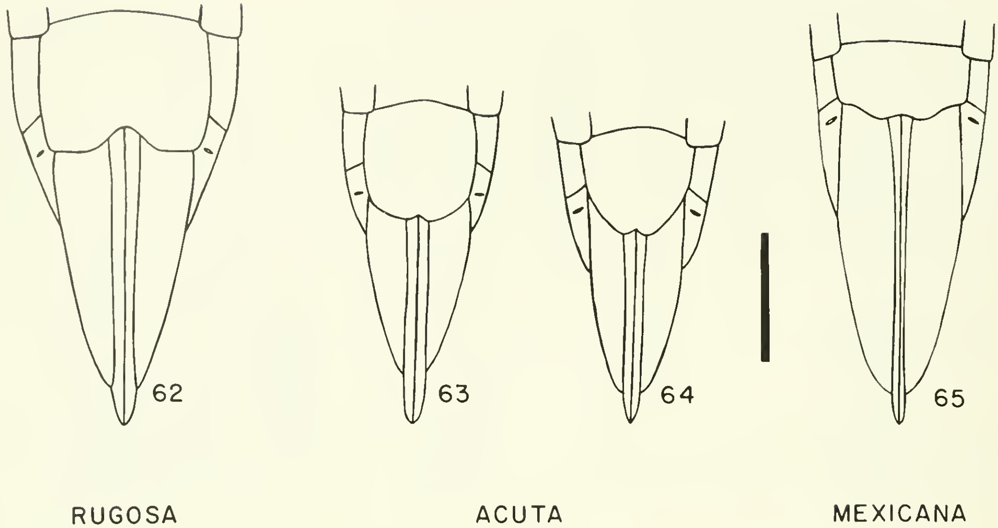
*Calliscarta corvenda* Kramer 1963: 210. (Covendo, La Paz, Bolivia, U.S. National Museum).

Length of male 9–9.8 mm.; female unknown. Color pattern similar to *stagmata*, except spots of forewings not forming rows or bands.

MALE GENITALIA.—Pygofer narrowing to inwardly hooked and pointed apex (Fig. 51). Genital plate large, expanded on apical half (Fig. 51). Style very elongate, hooked apically, with pointed, upturned apex (Fig. 54). Aedeagus semitubular, pair of lateral processes on ventral margin near middle of shaft, gonopore subapical on ventral margin (Figs. 52, 53).

TYPE.—Holotype (male), BOLIVIA, Covendo, August 1921, Mulford Biol. Expedition, Wm. M. Mann Coll., U.S. National Museum.

DISTRIBUTION.—Four specimens are known, including the type and a paratype from




Figs. 62–65. *Calliscarta* spp., ventral view of female segments: 62, *C. rugosa*, n. sp., holotype; 63, *C. acuta*, n. sp., holotype; 64, *C. acuta*, n. sp., paratype; 65, *C. mexicana*, n. sp., holotype. All drawn to the same scale; the line equals 1 mm.

Bolivia. Other specimens: VENEZUELA, two males, Barinitas, 15 km SW Barinas, 25 February 1969, Duckworth and Dietz Coll., one in U.S. National Museum and one in University of Kentucky Collection.

*Calliscarta rugosa*, n. sp.
Figs. 62, 68

Resembling *columbiana* in general color pattern, but with lighter, more reddish brown markings.

Length of female 10.1 mm; male unknown. General color pattern as in *columbiana*, but with forewing darker and more reddish brown.

FEMALE GENITALIA.—Seventh sternum large, truncate, with a large, median, U-shaped emargination (Fig. 62). Ovipositor extending its length beyond pygofer.

TYPE.—Holotype (female), VENEZUELA, Aragua, El Limón, 450 m, 23 August 1979, Luz de Mercurio, F. Fernandez Y. Coll., University of Central Venezuela Collection.

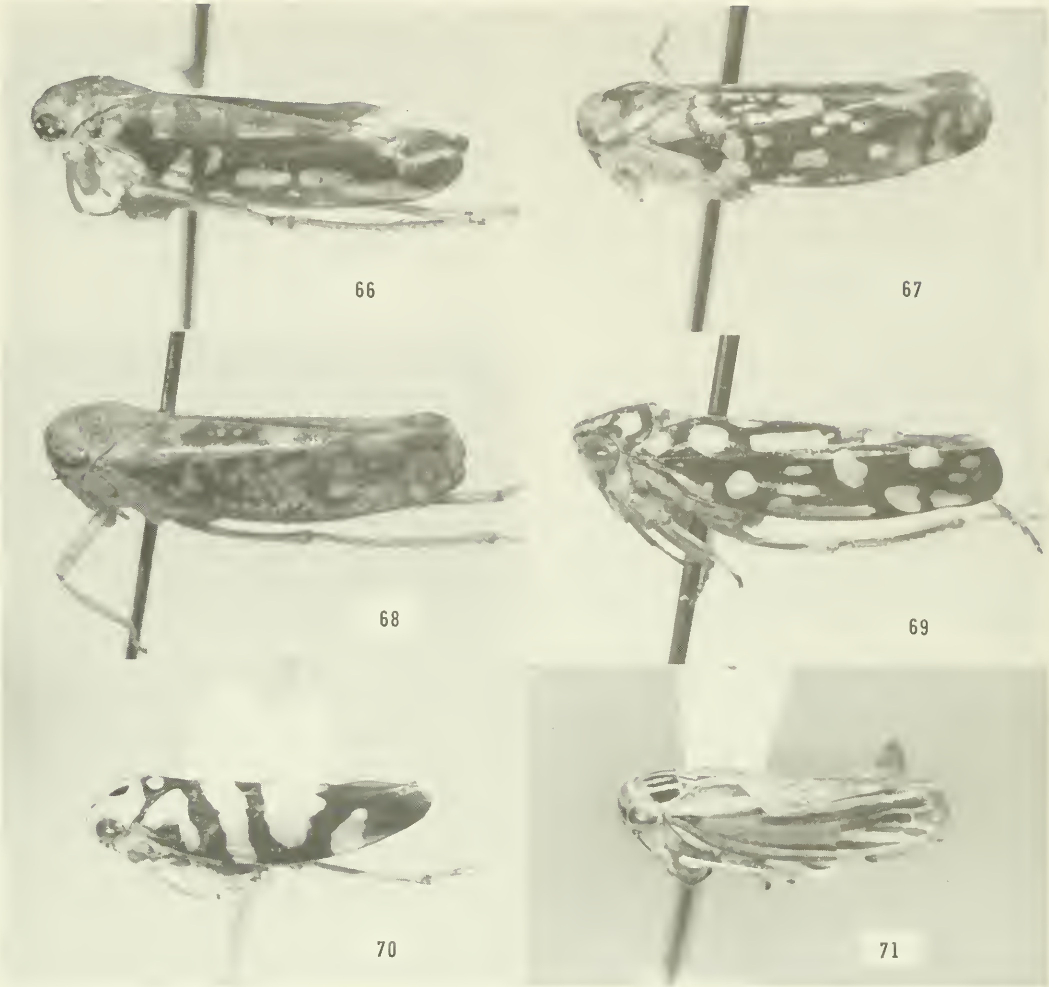
NOTES.—This female may be the female of *columbiana* or *corvenda*. However, since it was collected along the northern mountains of Venezuela, it is just as likely to represent a separate species. The color pattern is sufficiently different from the known species of the *stigmata* species group to warrant its description at present.

The following two species are not placed in a species group at this time, as the males are unknown and the color patterns give little indication as to how these relate to other known species. However, they are closer to the preceding groups than to the group following them.

*Calliscarta marginata*, n. sp.
Figs. 60, 69

This species resembles *ornata*, but with a brighter color pattern and the anterior margin of the crown more distinct.

Length of female 10.5 mm; male unknown. Head creamy yellow with a U-shaped band in middle of crown, a wider U-shaped band behind eyes over ocelli and along anterior margin, two transverse bands between antennae and ocelli, two dashes in middle of lower part of postclypeus, and a V-shaped band from underneath eyes along lateral margins of postclypeus down middle of anteclypeus, black. Pronotum black, with a yellow longitudinal band down median; also a large, yellow spot on each side with a smaller cream spot near anterior margin between yellow spot and band. Scutellum black, with cream spots. Forewing black, with six large, yellow spots or dashes on clavus, eight large, yellow spots or dashes on corium, and four smaller cream spots in apical cells.




Figs. 66–71. *Calliscarta* spp., lateral aspect: 66, *C. decora* (Fabricius), male from Peru; 67, *C. ornata*, n. sp., male paratype from French Guyana; 68, *C. rugosa*, n. sp., female holotype; 69, *C. marginata*, n. sp., female holotype; 70, *C. acuta*, n. sp., female holotype; 71, *C. mexicana*, n. sp., female holotype.

FEMALE GENITALIA.—Seventh sternum large, with posterior margin with a median, V-shaped emargination (Fig. 60). Ovipositor extending beyond pygofer three times its width.

TYPE.—Holotype (female), HONDURAS, Com., Lago Yojoa, 19 July 1974, C. W. and L. B. O'Brien and Marshall Coll., the Ohio State University Collection.

NOTES.—This species is quite distinct from other members of the genus both in color pattern and in having a slight anterior margin of the head.

*Calliscarta acuta*, n. sp.
Figs. 63, 64, 70

Resembling *marginata*, this species is smaller and has a distinctly different color pattern.

Length of female 8.9–9 mm; male unknown. Head creamy yellow, with a spot on either side of median near posterior margin of crown, a spot on either side of median on anterior margin of crown, an area around antennae down lateral margins of postclypeus, lora, and anteclypeus black. Pronotum creamy yellow with a large spot either side of median. Scutellum black with a median, orange spot. Forewing green, with three black bands, one at end of scutellum, one across middle, and one at end of clavus, apical cells black.

FEMALE GENITALIA.—Seventh sternum

large, roundedly produced, with a small, median, V-shaped emargination (Fig. 63). Ovipositor extending beyond pygofer nearly twice its width.

TYPE.—Holotype (female), VENEZUELA, T. F. Amazonas, 20 December 1981, eacuri, G. Yepez Gil Coll., University of Central Venezuela Collection. Paratype (female), PERU, Quincemil, August 1962, Luis E. Peña Coll., Ramos Collection.

NOTES.—The striking color pattern makes this species easy to identify. The two specimens differ slightly in color pattern and in the shape of the female genitalia, but this is probably individual variation as they come from quite different localities.

The *fasciata* species group is characterized by the longitudinal bands on the pronotum and the unusual, extra apodemal process on the aedeagus. The following two species belong to this group.

### *Calliscarta fasciata* (Osborn)
Figs. 55–58, 61

*Idiotettix fasciatus* Osborn 1929: 466. (Hohenau, Itapua, Paraguay, Ohio State University Collection); Oman 1938: 395; Evans 1947: 190; Nast 1952: 1; Maldonado Capriles 1954: 248; Metcalf 1966: 226.

*Calliscarta fasciata:* Linnavuori 1959: 30.

*Idiotettix brunneus* Osborn 1929: 467. (Hohenau, Itapua, Paraguay, Ohio State University Collection); Oman 1938: 395; Nast 1952: 1; Maldonado Capriles 1954: 248; Metcalf 1966: 226. *New synonymy*

*Calliscarta brunnea:* Linnavuori 1959: 32.

*Idiotettix lautus* Nast 1952: 3. (Porto Epitacio, São Paulo, Brazil, Polish Museum of Zoology); Maldonado Capriles 1954: 248; Metcalf 1966: 227.

Length of male 8–9.5 mm; female 9.8 mm. Head yellow, with a transverse band above ocelli, one below ocelli, a spot on each antennal ledge, a pair of longitudinal bands on postclypeus, and much of gena and lora orange; a row of brown or black transverse lines on each side of postclypeus. Pronotum yellow, with anterior margin, four wide, longitudinal bands, and lateral margins orange. Scutellum yellow, with orange-brown longitudinal band down median. Forewings orange fading to smoky brown at apex; claval and discal veins bordered with translucent purple bordered with dark brown, apical half with large, irregularly shaped white spots bordered with brown, apical cells with whitish, translucent spots. Ventral surface mostly yellow.

MALE GENITALIA.—Pygofer large, truncate, with a long process from ventral margin (Fig. 55). Genital plate large, expanded apical half, bluntly rounded at apex (Fig. 55). Style short, slightly curved laterad, with a pointed apex (Fig. 58). Aedeagus stout, curved dorsad apically, with a pair of lateral flanges from base of shaft to near apex, extra apodeme at base connecting aedeagus to anal tube (Figs. 56, 57).

FEMALE GENITALIA.—Seventh sternum greatly enlarged, rounded on posterior margin with a V-shaped, median emargination (Fig. 61). Ovipositor extending beyond pygofer its own width. Pygofer narrowed on apical third.

TYPE.—Holotype (male), PARAGUAY, Hohenau, Ohio State University Collection.

DISTRIBUTION.—This species is known from several hundred specimens from Brazil, Paraguay, and Peru. The only known female is in the University of Kansas Collection.

NOTES.—Linnavuori (1959) placed *lautus* as a synonym of *fasciatus*. The type of *brunnea* represents the teneral form of this species; consequently, it is placed in synonymy.

### *Calliscarta mexicana*, n. sp.
Figs. 65, 71

This species resembles *fasciata*, but it is smaller and the apical area of the forewing is without large, transparent spots.

Length of female 8 mm; male unknown. Head creamy yellow, with a large, orange transverse band across middle of crown, an orange transverse band just below ocelli with ends below ocelli dark brown, an orange-brown transverse band across postclypeus halfway between antennae and ocelli with extensions down both sides of postclypeus as a brown longitudinal band to anteclypeus, and a dark brown area around bases of antennae extending along lateral margins of postclypeus. Pronotum creamy yellow with four wide, orange-brown longitudinal bands, median pair extending as brown longitudinal bands on scutellum. Forewing orange-brown with longitudinal bands of creamy white, one along costa, one along claval vein on clavus, one along commissure, as well as white areas along apical longitudinal veins.

FEMALE GENITALIA.—Seventh sternum slightly enlarged, with posterior margin roundly produced with a slightly rounded median emargination (Fig. 65). Ovipositor extending only slightly more than its width beyond pygofer.

TYPE.—Holotype (female), MEXICO, Tamazunchale, S. L. Potosi, 19 June 1941, Henry S. Dybus Coll., Field Museum.

NOTES.—This species is very similar to *fasciata* in overall color pattern. These two species form a species group that is quite different from the other species of this genus.


## ACKNOWLEDGMENTS

Material for this study has been gathered over the last 20 years from the institutions listed below. I certainly thank the curators for their patience over these long years, for the loan of these most valuable specimens, and also for the opportunity to study type material: American Museum of Natural History, New York City, Dr. Jerome G. Rozen, Jr., and Dr. Randall T. Schuh; Carnegie Museum, Pittsburg, Dr. Chen W. Young; Field Museum of Natural History, Chicago, Dr. R. Wenzel; Ohio State University, Columbus, Dr. Charles A. Triplehorn; Muséum National d'Histoire Naturalle, Paris, Dr. Michel Boulard; Ramos Collection, Mayaguez, Dr. J. A. Ramos; United States National Museum, Washington, D.C., Dr. James P. Kramer; University of Kansas, Lawrence, Dr. George W. Byers and Dr. Peter D. Ashlock; Universidad Central de Venezuela, Instituto de Zoologia Agricola, Maracay, the late Dr. F. J. Fernandez-Yepes.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# A NEW SPECIES OF *PAZU* OMAN FROM EASTERN CALIFORNIA (HOMOPTERA: CICADELLIDAE: DELTOCEPHALINAE)

Raymond J. Gill[1]

ABSTRACT.—A new species of *Pazu*, *P. monoinyo*, from the Inyo-Mono County area of California is described. Additional occurrence records are provided for *Pazu balli* (Beamer), and some of its morphological characteristics are illustrated and compared with *P. monoinyo*.

The monobasic genus *Pazu* was erected by Oman (1949) to include *Hebecephalus balli* Beamer (1946) from central Arizona. *Pazu* is distinguished from *Hebecephalus* primarily by the shape of the styles, which in *Hebecephalus* have the apical portion bent laterad to the shaft at right angles, forming an elongate, slender "toe." The type species of *Pazu* and the new species described here have more conventional, straighter styles (see Figs. 1E and 2E).

Specimens of this new taxon were collected from antifreeze (ethylene glycol) pitfall traps placed in sandy areas or on small sand dune habitats in a 78-km$^2$ area in Inyo and Mono counties near Bishop, California, and from a single location 42 km east of Bishop near Deep Springs. The area is semiarid Great Basin habitat irrigated in the lower areas by snowmelt runoff from nearby mountain peaks or from artesian springs. The traps were placed at these and other sand dune locations throughout the southwestern U.S. as part of a joint project between the California Department of Food and Agriculture and the U.S. Bureau of Land Management (BLM) (Andrews et al. 1979). The purpose of the project was to study the insect fauna associated with sand dune habitats as part of an effort by the BLM to preserve sand dune habitats.

The fact that all known specimens of *P. monoinyo* exhibit microptery and have been collected from just three pitfall trap locations indicates that the species may spend considerable time on the soil surface and on the crowns of the host rather than on aerial plant parts. Whether a fully macropterous form capable of flight actually exists in certain situations is unknown. A macropter collected at Blythe, Riverside County, California, on 2-IV-63 is nearly identical in color pattern to *P. monoinyo;* however, the specimen is missing the abdomen, thus making accurate identification impossible. If such a form does exist, it is probably not common and may explain why the species has previously gone undetected. In all collection locations the dry sand dune habitats were in close proximity to water and the lush vegetative growth associated with it. The dune site east of Bishop, California, is within 100 m of the Owens River; the Fish Slough and Deep Springs locations are adjacent to a series of artesian springs. Since the species has not been collected from other sand dune localities, it would appear that the species lives and feeds in or on the crowns of plants, presumably grasses, near permanent sources of surface water. However, several attempts to re-collect the species at two of the known localities have failed.

## *Pazu monoinyo*, n. sp.

DESCRIPTION.—Resembles *P. balli* (Beamer) but with darker, more distinct markings and different genitalia.

EXTERNAL CHARACTERISTICS.—Ground color apparently cinereous, although the possible color-altering effects of the antifreeze and alcohol preservatives leave the actual color in doubt. Markings fuscous. Crown with a broad, longitudinal pair of lines, each with a central cinereous line, so that the markings appear as two pairs of fuscous lines on either side of the midline; with a fuscous spot between each ocellus and compound eye. Frons

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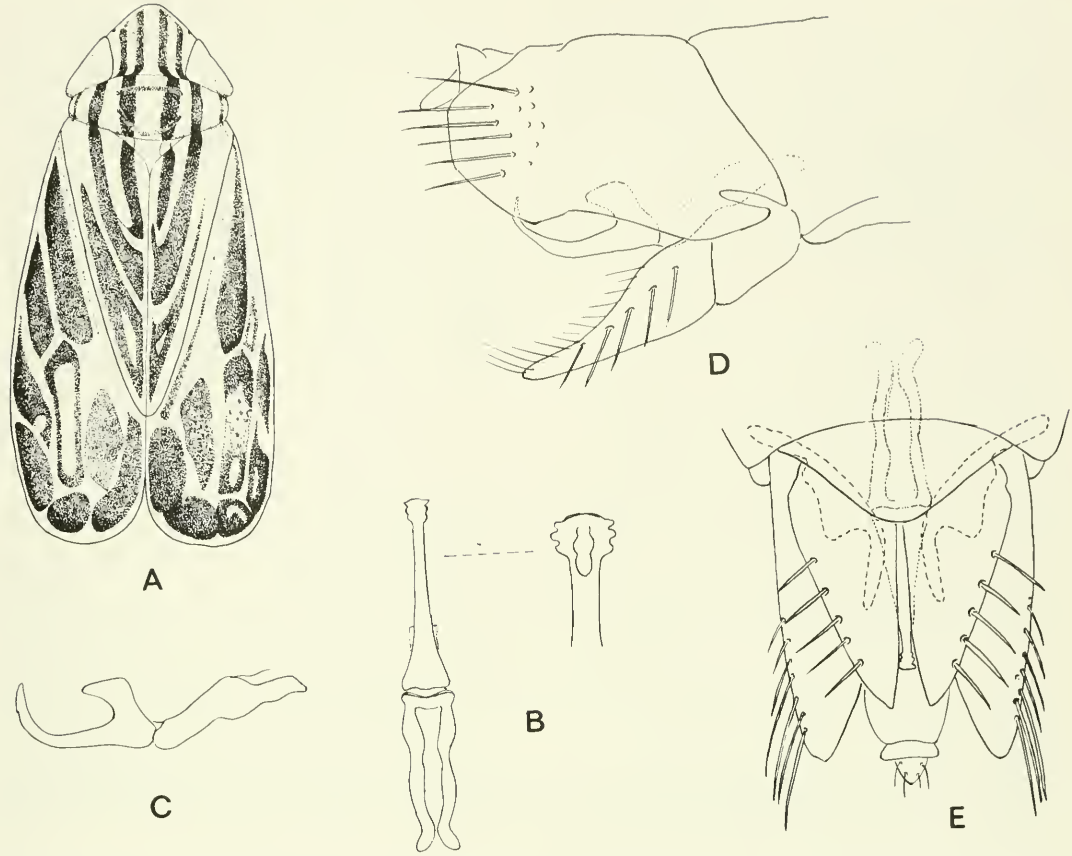


Fig. 1. *Pazu monoinyo*, n. sp.: A, adult female habitus; B, male aedeagus and connective, dorsal view; C, male aedeagus and connective, lateral view; D, apex of male abdomen, lateral view; E, apex of male abdomen, ventral view.

with two pairs of arclike, subapical, fuscous markings and occasionally with a pair of rectangular, basal, fuscous spots next to clypeus; frons apparently never clouded with fuscous as in *P. balli*. Thorax with six fuscous, longitudinal lines, thickest lines medial, all lines lighter than those on crown. Abdominal dorsum with three pairs of longitudinal, fuscous lines, the lateral pairs often coalescing to form bands twice the width of medial pair. Venter cinereous variously marked with fuscous, especially on anterior median areas of sternites. Legs cinereous with two or more fuscous spots or bars on femora, other leg segments darker near spines and at spine bases. Elytra reduced (micropterous as delineated by Oman 1987), barely reaching ninth abdominal segment. Most elytral cells filled to a greater or lesser degree with fuscous; all veins or cells on either side of claval vein usually clear or white. Wings reduced, ca 1/2 x length of elytra. There appears to be no color or other dimorphisms between the sexes.

MALES.—Length 3.4–3.7 mm (mean 3.6 mm), specimens slightly shriveled due to preservation methods. Wing length 2.4–2.7 mm (mean 2.6 mm); vertex length 0.4–0.6 mm (mean 0.5 mm); transocular width 1.0–1.3 mm (mean 1.2 mm); interocular width 0.4–0.6 mm (mean 0.6 mm). Pygofer shorter than in *P. balli*, more truncated, with just a vestige of a tooth on lateroventral corners; weakly setose. Plates evenly tapered to acute apices and completely divided, not basally fused and truncate as in *P. balli;* spinelike setae uniseriate. Style apices J-shaped, medial apex long, slender, very slightly curved laterad; lateral tooth broadly triangular. Connective linear, about as long as aedeagal shaft. Aedeagus roughly V-shaped; anterior arm broader, apex curved posteriorly;

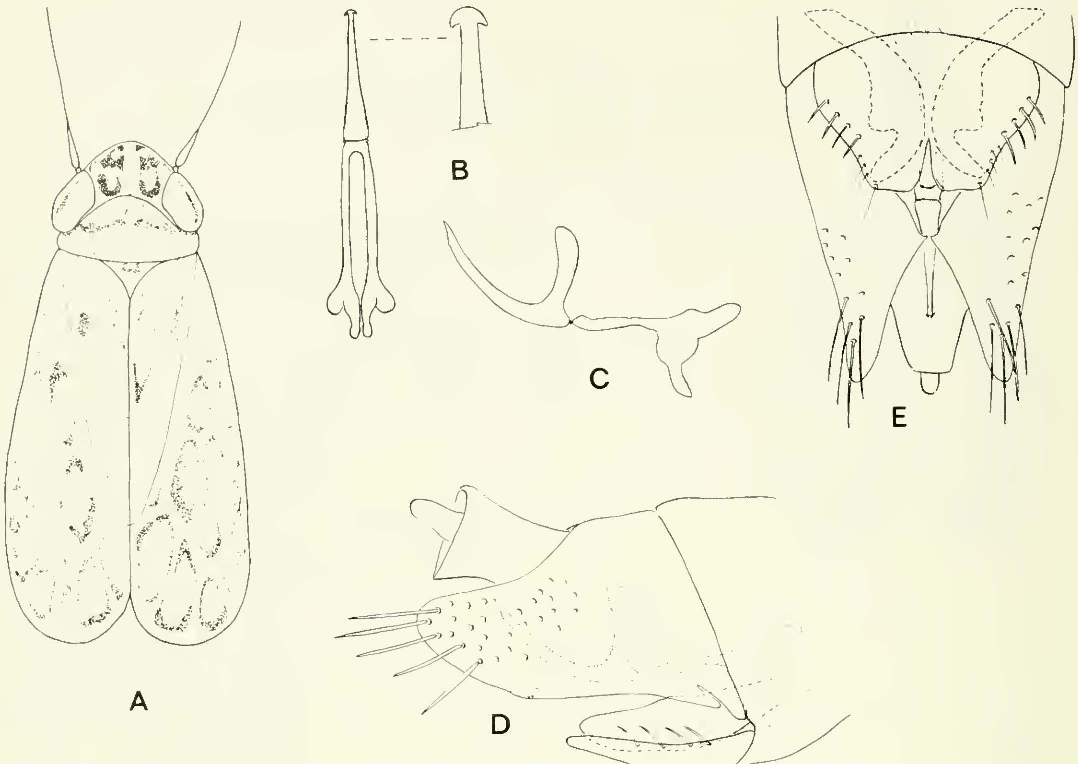


Fig. 2. *Pazu balli* (Beamer): A, adult female habitus; B, male aedeagus and connective, dorsal view; C, male aedeagus and connective, lateral view; D, apex of male abdomen, ventral view.

posterior arm ca 1/2 x width of anterior, gradually and evenly tapered to apex, crescentic in lateral view. Aedeagal apex with three pairs of apicolateral flanges or blunt teeth.

FEMALES.—Length 4.6–5.0 mm (mean 4.6 mm). Wing length 2.9–3.1 mm (mean 3.0 mm); vertex length 0.7–0.9 mm (mean 0.7 mm); transocular width 1.4–1.6 mm (mean 1.4 mm); interocular width 0.6–0.9 mm (mean 0.6 mm). Last ventral segment with broadly rounded, posteriorly directed median lobe.

ETYMOLOGY.—The name *monoinyo* is a noun in apposition referring to the two localities where the species was collected, Mono and Inyo counties, California.

DISCUSSION.—*Pazu monoinyo* is similar to the generic type, *P. balli*, in color pattern and male genitalia. Color patterns differ in that the dorsal, longitudinal lines tend to be much darker and more distinct on the head and thorax in *P. monoinyo*, but much lighter and with a tendency to coalesce in *P. balli*. The male genitalia differ in that the pygofer is much shorter in *P. monoinyo;* the plates are completely divided and have acute apices in *P. monoinyo* compared with basally fused, truncate plates in *P. balli*. The last ventral segment of the female is lobed posteriorly in *P. monoinyo* but deeply cleft in *P. balli*. All known specimens of *P. monoinyo* exhibit microptery, whereas all those of *P. balli* are macropterous.

Specimens of *P. balli* are known from Cochise and Pearce, Cochise County, Arizona.

MATERIAL EXAMINED.—Male holotype and female allotype: "Calif., Mono Co., 9 mi N Bishop, Fish Slough, 4,200′, sand dunes, V-12-82 to XII-20-82, Derham Giuliani, collected in ethylene glycol pit trap." Paratypes: "Calif., Mono Co., 9 mi N Bishop, Fish Slough, 4,200′, sand dunes, V-12-82 to XII-20-82, Derham Giuliani, collected in ethylene glycol pit trap," 4 males and 2 females; "Calif., 3 mi E Bishop, 4,100′, sand dunes,

V-12-82 to XII-10-82, antifreeze pit trap, D. Giuliani," 1 male and 4 females; "Inyo Co., Ca., Deep Springs Valley, VI-9-78, antifreeze pit trap, D. Giuliani," 1 female.

TYPE DEPOSITION.—The holotype and allotype (both CAS Type #16039) were deposited in the California Academy of Sciences, San Francisco (CAS). Twelve paratypes were deposited as follows: 2 males, 2 females, San Francisco (CAS); 2 males, 4 females, California Department of Food and Agriculture, Sacramento (CDFA); 1 male, 1 female, United States National Museum, Washington, D.C. (USNM).


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I express gratitude to Dr. Leon W. Hepner, Mississippi State University, State College, Mississippi, and to Dr. Steve Wilson, Central Missouri State University, Warrensburg, Missouri, for reading the manuscript and offering useful suggestions. I also thank Dr. Robert Brooks, Snow Entomological Museum, Lawrence, Kansas, for the loan of the type specimens of *Pazu balli*. I am extremely grateful to Susan Sawyer, CDFA, for the habitus sketches of *Pazu monoinyo* and *Pazu balli*.


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# EVIDENCE FOR AN INDO-PACIFIC ORIGIN OF HAWAIIAN ENDEMICS IN *BALCLUTHA* AND RELATED GENERA (CICADELLIDAE: MACROSTELINI)

W. J. Knight[1] and M. D. Webb[1]

ABSTRACT.—The 10 endemic species of *Balclutha* in Hawaii are reviewed and compared with the Pacific and American forms of the genus. Two new species, *nigriventris* and *fuscifrons*, are described; *kilaueae* is transferred to a new genus *Balolina* n. comb.; *beardsleyi* is synonymized with *saltuella*, n. syn.; and *hospes* is relegated to a subspecies of *incisa*, n. stat. Descriptions and notes, together with illustrations and a key, are given for each taxon. Evidence is presented to suggest that all the endemic species of *Balclutha* have arisen within the islands from a single colonization and that the taxon showing the greatest similarity to them is the widespread Pacific species *B. lucida*. It is shown that the Hawaiian genus *Nesolina* is most closely related to the endemic species-group of *Balclutha* and that *Balolina* is an independent colonization.

The isolated position, volcanic origin, and diverse habitats of Hawaii, together with the division of the area into several large islands, have combined to produce a depauperate, yet large and highly endemic, biota (Simon 1987). This phenomenon is well illustrated by the plant-feeding insect family Cicadellidae. The family was studied in the islands by Kirkaldy (1910) and Osborn (1935) and subsequently reviewed by Zimmerman (1948). Namba (1956) later described several new species.

In his review of the Hawaiian insect fauna, Zimmerman (1948) considered the generic affinities to be predominantly Pacific and only 5% American. The Homoptera were considered to be exclusively Pacific, although little evidence was provided.

Compared with the Pacific and mainland America, the Hawaiian cicadellid fauna is very depauperate at the supraspecific level. Only 5 of the 35 subfamilies are present, 4 of which are represented by 5 recently introduced species from North America. In contrast, the Deltocephalinae, a large, worldwide group with 17 currently recognized tribes, is represented by 2 tribes. The endemic genera *Nesophryne* (2 species), *Kirkaldiella* (2 species), and *Nesophrosyne* (60 species) belong to the Opsiini and are related to the Pacific genus *Orosius* (Linnavuori 1960, Ghauri 1966). *Nesolina* (1 species), *Balolina* n. gen. (1 species), and the cosmopolitan genus *Balclutha*, comprising 105 species and represented in Hawaii by 11 endemic and 2 cosmopolitan species, belong to the Macrostelini, the major cicadellid group in the similarly isolated islands of Marquesas in the Pacific, and St. Helena in the Atlantic. This tribe contains approximately 30 genera worldwide, of which 10 are island endemics, 2 in Hawaii, 4 in the Marquesas, and 4 on St. Helena. Interestingly, although the main host plants of the group are Gramineae, in Hawaii, Marquesas, and St. Helena shrubs and tree ferns of southern temperate distribution are also utilized (Webb 1987).

## MATERIALS

The material studied is primarily from the Bishop Museum, together with some in the British Museum (Natural History), abbreviated throughout the text to BPBM and BMNH, respectively.

## METHODOLOGY

The present study investigates the origins of the Hawaiian *Balclutha* species. This has necessitated a reexamination of all the Hawaiian species and a review of the variation in characters among Pacific and American species of the genus. Until a phylogenetic analysis of the genus and tribe is undertaken, any statements on the polarity of characters within these taxa would be premature. Our biogeographical inquiry is therefore based on phenetic resemblances rather than on shared

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apomorphies and should be seen as only exploratory and preliminary in nature.

## FAUNAL RELATIONSHIPS OF HAWAIIAN *BALCLUTHA*

The variation in morphological characters in *Balclutha* was reviewed by Knight (1987) for the south and west Pacific species and by Blocker (1967) for the American species. Both faunas are of comparable size, 30 and 32 species, respectively, but have only 3 species in common, *saltuella*, *incisa*, and *lucida*.

Compared with the Pacific and American species, the 10 endemic Hawaiian species, *nigriventris* n. sp., *fuscifrons* n. sp., *grandis* Namba, *phoxocephala* Namba, *timberlakei* (Osborn), *lobata* Namba, *usitata* Namba, *volcanicola* (Kirkaldy), *plutonis* (Kirkaldy), and *peregrina* (Kirkaldy), differ only slightly from each other in head shape and minor details of the male genitalia, suggesting that they probably arose from one founder species. The character states common to the 10 endemic species are listed below, the condition present in the 10 endemic species shown in italics:

1. Relative width of head and pronotum: *head equal to or wider than the pronotum.*
2. Length of vertex: *longer medially than next to eyes.*
3. Laterofrontal sutures: *terminating at or near the ocelli.*
4. Distance between ocelli and eyes: *ocelli separated from the eyes by a distance equal to 2–4 times their own diameter.*
5. Foretibia setal formula: *1.3.*
6. Hind femora setal formula: *2.1.1.*
7. Shape of male pygofer: *simple, without ventral lobes or processes.*
8. Shape of subgenital plates: *triangulate, with apical, fingerlike process 1/4–1/2 total length of plate.*
9. Shape of styles: *robust, with apical process and preapical lobe well developed.*
10. Relative length of stem and arms of connective: *stem longer than arms.*
11. Shape of aedeagal shaft: *simple, elongate, curving dorsally or anterodorsally to point level with or slightly anterior to atrium.*

### Comparison between the Hawaiian, Pacific, and American Species

In the present section, the Pacific and American species of the genus are reviewed for each of the characters listed above. The alternative conditions of characters 3, 5, and 7 are coded A and B for ease of reference in subsequent discussion.

The relative width of the head (character 1) varies within the genus and may be wider, equal to, or narrower than that of the pronotum. All three conditions are present in both the American and the Pacific faunas, half the species in each region showing the head approximately equal to or wider than the pronotum, as in Hawaii.

The vertex (character 2) is usually short and uniform in length and is one of the main distinguishing features of the genus. The medial prolongation of the vertex found in the Hawaiian species occurs in the Pacific in only *smaragdula*, and in a few individuals of *flagellata*, *bifasciata*, *rieki*, and the cosmopolitan species *punctata*. It is far more prevalent among the American forms, being a characteristic feature of 7 species and occurring occasionally in 15 others.

The laterofrontal sutures (character 3) usually terminate at or near the ocelli (condition B) but are occasionally turned medially, ventrad of the ocelli (condition A). With the exception of *simplex* and the cosmopolitan *saltuella*, the Pacific species have the sutures terminating near the ocelli as in Hawaiian species. Both conditions also occur in the American fauna but with an approximately equal number of species of each.

The ocelli (character 4) are usually small and situated on the anterior margin of the head, separated from the corresponding eye by approximately their own diameter. Most of the American and Pacific species have the ocelli in this position, or only slightly more remote from the eye. Only *impicta* and *arctica* in America, *flagellata* and *cheesmanae* in the Pacific, and the cosmopolitan species *punctata*, have the ocelli more than twice their own diameter from the eyes, and approximating the condition found in Hawaiian species. The Pacific fauna shows greater flexibility in this character, however, with *chloroptera* and *bulbosa* having the ocelli enlarged and more dorsad in position.

Throughout the genus, the foretibia setal formula (character 5) may be 1.1 (condition A), 1.3 (condition B), or rarely 1.4. The condition in Hawaii (condition B) is similar to that in the majority of Pacific species. Only two Pacific species, *simplex* and the cosmopolitan *saltuella*, show condition A. In the American fauna, half of the species examined have condition A and half condition B.

The setal pattern at the apex of the hind femora (character 6) varies within the genus from 2.1.1 to 2.2.1. The two conditions occur equally throughout both the Pacific and American faunas, unlike Hawaii where only the former is found.

The male pygofer (character 7) varies from a simple, rounded shape (condition A), as found in Hawaii, to a more complex form with posteroventral lobes or processes (condition B). The simple form is rare outside Hawaii, occurring in only *simplex* in the Pacific and in the species *lucida* and *saltuella*, which occur in both regions.

The subgenital plates (character 8) are characterized in all species by a membranous, fingerlike, apical segment. The shape of the plate found in the Hawaiian species occurs in the majority of Pacific and American species, being slightly more prevalent in the latter region. The remaining species in both regions have the basal part of the plate much reduced in size.

The robust, well-developed styles (character 9) of the Hawaiian species occur in the majority of species in both the Pacific and America but are more widespread in the former. Only two Pacific species, *bulbosa* and *rieki*, have a reduced style, compared with nine species in the Americas, plus the cosmopolitan *saltuella* in both regions.

The Y-shaped connective (character 10) varies principally in the relative length of the stem and arms. The condition present in Hawaii, with the stem longer than the arms, is present in 50% of the species in the Pacific but in only 30% of the species in America.

A simple, filamentous aedeagus (character 11) is characteristic of the majority of species in the genus. In the Hawaiian species the shaft is directed dorsally or curved anterodorsally to a point approximately level with the well-developed, basal apodeme, a form that occurs in 50% of the fauna in both the Pacific and America.

## Faunal Similarity

If we take the number of species in each region showing character states identical with those in Hawaii as a measure of similarity, then the Hawaiian species show greater similarity to the Pacific fauna with respect to the laterofrontal sutures, foretibial setal pattern, styles, connective, and to a lesser extent the ocelli and male pygofer. The American species show greater similarity only in the length of the vertex and to a lesser extent in the shape of the subgenital plates. The relative width of the head, the setal pattern on the hind femora, and the shape of the aedeagus provide little information in this respect. If we eliminate those characters that confer only minimal regional preference, such as the ocelli, male pygofer, and subgenital plates, and also those known to vary infraspecifically, such as the length of the vertex, we are left with only four, the laterofrontal sutures, the foretibial setal pattern, and the shape of the styles and connective, all of which support the theory of closer links with the Pacific.

Further support for a Pacific link is provided by the Sorensen Coefficient of Similarity (Southwood 1978)

$$Cs = 2j/(a + b)$$

where j is the number of character states common to the two areas and a + b are respectively the number of character states in each area. Based on the endemic species in each area, the coefficient for Hawaii and the Pacific is 0.74 and for Hawaii and the Americas is 0.58, showing a greater degree of similarity between the first two areas.

From the above review it is seen that no one character is shared exclusively between Hawaii and either of the other two regions to provide evidence of affinity. However, if we consider a combination of characters, rather than single characters alone, then the picture becomes a little clearer.

Table 1 shows the Pacific species and their similarity or dissimilarity to the Hawaiian endemic species with regard to the 11 characters. This reveals an obvious correlation between characters 3, 5, and 7. All three characters show condition A[2] in the first two species and condition B[2] in the fourth species onward. An intermediate stage occurs in the third species, *lucida*, which has condition B in characters 3 and 5 but retains condition A in character 7. The American species show the same correlation between characters 3, 5, and 7, but, except for *lucida*, the character states in the intermediate stage are reversed. This is shown in Table 2, where the intermediate stage is highlighted for each region. The similarity between the Hawaiian endemics and *lucida* in this respect is unique.

[2]See previous section, paragraphs 4, 6, and 8.

TABLE 1. A list of the Pacific species of *Balclutha*, showing the similarities (+) and differences (−) between them and the Hawaiian endemics for the 11 listed characters. (For further explanation, see text.)

| Pacific species | Characters 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *saltuella* | + | − | − | − | − | + | + | − | − | − | + |
| *simplex* | + | − | − | − | − | + | + | − | + | − | + |
| *lucida* | + | − | + | − | + | + | + | + | + | − | − |
| *bilobata* | − | − | + | − | + | + | − | − | + | − | − |
| *batuensis* | + | − | + | − | + | − | − | + | + | + | + |
| *punctata* | − | ± | + | + | + | − | − | + | + | + | + |
| *neglecta* | + | − | + | − | + | + | − | + | + | − | + |
| *viridinervis* | + | − | + | − | + | − | − | + | + | ± | − |
| *flagellata* | − | ± | + | + | + | − | − | + | + | ± | − |
| *bifasciata* | + | ± | + | − | + | + | − | − | + | + | + |
| *trilineata* | ± | − | + | − | + | − | − | + | + | − | − |
| *rieki* | + | ± | + | − | + | + | − | − | − | − | + |
| *cheesmanae* | − | − | + | + | + | − | − | + | + | + | − |
| *yanchepensis* | ± | − | + | − | + | − | − | + | + | + | + |
| *smaragdula* | − | + | + | + | + | + | − | − | + | + | + |
| *alstoni* | + | − | + | − | + | − | − | + | + | + | + |
| *kuroiwae* | + | − | + | − | + | ? | − | − | + | + | + |
| *asymmetrica* | − | − | + | − | + | ? | − | + | + | − | − |
| *chloroptera* | − | − | + | ± | + | − | − | + | + | + | − |
| *bulbosa* | − | − | + | ± | + | − | − | + | − | + | − |
| *bacchusi* | + | − | + | − | + | + | − | + | + | + | + |
| *spiniloba* | + | − | + | − | + | ? | − | + | + | + | + |
| *incisa* | + | − | + | − | + | + | − | + | + | + | − |
| *rosea* | + | − | + | − | + | + | − | + | + | − | + |
| *pseudorosea* | + | − | + | − | + | + | − | + | + | − | + |
| *rubrostriata* | + | − | + | − | + | + | − | + | + | + | + |
| *wilsoni* | − | − | + | − | + | − | − | + | + | − | − |
| *distenda* | − | − | + | − | + | − | − | + | + | − | − |
| *rubrinervis* | − | − | + | − | + | − | − | + | + | − | − |
| *noonadana* | ± | − | + | − | + | − | − | + | + | − | − |

TABLE 2. Character-state distribution for three characters in Pacific and American species of *Balclutha*. (For further explanation, see text.)

| Pacific species | Characters 3 | 5 | 7 | American species* | Characters 3 | 5 | 7 |
|---|---|---|---|---|---|---|---|
| *saltuella* | A | A | A | *saltuella* | A | A | A |
| *simplex* | A | A | A | | | | |
| | | | | *neglecta* | A | A | B |
| *lucida* | B | B | A | *chiasma* | A | A | B |
| | | | | *sandersi* | A | A | B |
| remaining spp. | B | B | B | | | | |
| | | | | remaining spp. | B | B | B |

**lucida*, which occurs in Central and South America, has been omitted from this half of the table in the interests of clarity.

## Distribution of *B. lucida*

Since *lucida* is the species most similar to the Hawaiian forms, it is of interest to examine its distribution relative to Hawaii. Figure 53 shows its distribution, extending from the Aldabra Islands (Webb 1980 [*filum*]) in the west to Central and South America in the east (Blocker 1967 [*floridana*] and Knight 1987). It is a tropical and semitropical species clearly capable of movement over long distances and with the ability to colonize and establish itself on islands and mainland areas. Its presence in the Marshall and Marquesas islands places it within a comparatively short distance from Hawaii. The available data, however, provide no information on the center of origin for the species, although its absence from mainland Africa and Asia suggests that it is either the Pacific or Central America.

## RELATIONSHIP OF *BALCLUTHA* TO OTHER HAWAIIAN MACROSTELINI

In addition to *Balclutha*, two other macrosteline genera occur in Hawaii, both endemic.

The monotypic genus *Nesolina* differs from *Balclutha* principally in the more elongate head and the possession of longitudinal brown stripes on the vertex and pronotum. In all other characters it closely resembles the endemic species of *Balclutha* to which it is probably most closely related. Despite this close similarity, the present status of *Nesolina* is preserved, pending a phylogenetic study of the Macrostelini.

The relationship of the remaining Hawaiian macrosteline genus, *Balolina* n. gen., is uncertain. Although it is similar in general appearance to *Balclutha* and the Pacific genus *Nesoclutha* and has the first valvulae fused as in *Balclutha* (Fig. 33), it differs in many significant features, as listed below in the key and generic description. Except for the position of the ocelli, there is little to indicate that it is in any way related to the Hawaiian species of *Balclutha*. On the contrary, it appears to be an independent introduction to the islands.

All three Hawaiian macrosteline genera belong to a group having the hindwing veins sc and r united into a single vein, with a consequent reduction in the number of apical cells (Fig. 32). This is considered by Ossiannilsson (1983) to be justification for placing *Balclutha* in a separate tribe, the Balcluthini, which is also characterized (Oman 1949) by the possession of a sulcate hind basal tarsus (Fig. 74). Both characters are found to some degree, however, in other genera, including *Macrosteles*. The phylogeny of the Macrostelini proposed by Triplehorn and Nault (1985) includes *Balclutha* but omits several other genera, including the 10 island endemics. Some of these have been treated by Webb (1986, 1987).

## DISTRIBUTION OF HAWAIIAN MACROSTELINI

Table 3 summarizes previous (x) and new (N) distribution data and shows that the largest and youngest islands, Hawaii and Maui, respectively, support the most species, and that Kauai and Molokai, which differ considerably in size, have similar numbers of species. Further collecting on the islands may have profound effects on the distributional records and may even reveal further species.

## KEYS AND DESCRIPTIONS

The taxonomy of the Hawaiian Macrostelini has been treated by several authors (see introduction), but descriptions are usually incomplete and contain little information on intraspecific differences. Namba's (1956) revision of *Balclutha* was a considerable improvement on previous work, but a few of the characters referred to are unreliable. New keys to genera and species are given to take account of this and to accommodate the new taxa. All host records given below are taken from either Zimmerman (1948), Namba (1956), or specimens examined.

### Key to the Genera of Hawaiian Macrostelini

1. Head and thorax with longitudinal, brown bands; vertex elongate (Fig. 54) ....... *Nesolina*

— Head and thorax not marked as above; vertex short to moderately long (Figs. 7, 15) ........ 2

2(1). Vertex moderately long, ocelli situated almost to point midway between eye and midlength of foremargin of vertex (Fig. 67). Clypellus extending well beyond margin of face, transclypeal suture obscure; laterofrontal sutures short (Fig. 68). Foretibia with apical setae similar in length (Fig. 73). Hind femur with apical setal formula 2+2+1 (Fig. 69). Macrosetae of legs and genital segment nonhairy. Aedeagal shaft with pair of apical processes (Fig. 82); gonopore apical on ventral surface (Fig. 76). Connective with stem very short (Fig. 80). Subgenital plate with irregular macrosetae (Fig. 83). Second valvulae evenly tapered to apex; teeth extending over distal half of dorsal margin and onto apex of ventral margin (Fig. 75) ............................. *Balolina*

— Vertex short to moderately long; ocelli situated near eye or at point one-third distance from eye to midlength of foremargin of vertex (Figs. 2, 15, 28). Foretibia with apical setae dissimilar in length (Fig. 35). Hind femur with apical setal formula 2+1+1 (Fig. 30). Male and female genitalia not as above .............. *Balclutha*

### Key to Species of Hawaiian *Balclutha*

1. Vertex of uniform length; ocelli 1.0–1.5 times own diameter from corresponding eye; coronal suture visible in facial view (Figs. 28, 29) Pygofer lobe with a ventral process (Figs. 37, 46). Connective with arms equal in length to stem (Fig. 42) ........................... 11

— Not as above ........................... 2

2(1). Yellow to greenish yellow, marked with brown on first thoracic sternite (as in *saltuella*, Fig.

TABLE 3. Distribution of the Macrostelini on the Hawaiian islands, from the oldest in the north (left) to the youngest in the south (right).

| Area (sq km) | Kauai 1437 | Oahu 1564 | Molokai 673 | Lanai 365 | Maui 1885 | Hawaii 10437 |
|---|---|---|---|---|---|---|
| *Nesolina* | | | | | | |
| *lineata* | – | x | – | – | – | x |
| *Balolina* | | | | | | |
| *kilaueae* | x | x | x | – | x | x |
| *Balclutha* | | | | | | |
| *grandis* | x | – | – | – | – | – |
| *saltuella* | – | x | – | – | – | – |
| *phoxocephala* | x | x | x | – | – | – |
| *incisa hospes* | x | x | x | x | x | x |
| *timberlakei* | N | x | x | x | x | x |
| *lobata* | x | x | N | – | x | x |
| *usitata* | x | x | N | – | x | x |
| *volcanicola* | – | – | x | – | N | x |
| *plutonis* | – | – | – | – | x | x |
| *peregrina* | – | – | – | – | x | x |
| *nigriventris* | – | – | – | – | N | N |
| *fuscifrons* | – | – | – | – | N | – |
| Total | 7 | 8 | 7 | 2 | 10 | 11 |

43), abdomen (at least dorsally), and sometimes legs . . . . . . . . . . 3

— Not marked as above or if abdomen and first thoracic sternite marked with brown, then overall color yellow tinged with scarlet . . . . . . . 5

3(2). Large species, 4.0–4.4 mm in length. Aedeagus and style as in Figures 3, 4, 18 . . . . . . . . . . *fuscifrons*, n. sp.

— Small to moderately large species, up to 3.5 mm . . . . . . . . . . 4

4(3). Vertex marked with stramineous or brown (Figs. 5, 7). Aedeagal shaft robust (Fig. 24) . . . *volcanicola* (Kirkaldy)

— Vertex without markings. Aedeagal shaft slender (Fig. 19) . . . . . . . . . . *nigriventris*, n. sp.

5(2). Large species 4.5–5.3 mm in length. Stem of connective broad. Aedeagus as in Figure 21 . . . . . . . . . . *grandis* Namba

— Small to moderately large species, up to 4.0 mm . . . . . . . . . . 6

6(5). Preapical lobe of style large; apical process abruptly tapered distally (Figs. 16, 17). Female genital sternite marked with brown on disc (Fig. 8) . . . . . . . . . . *lobata* Namba

— Not as above . . . . . . . . . . 7

7(6). Moderately large species, 3.5–4.0 mm. Clypellus with sides concave. Connective elongate, longer than style (as in *timberlakei*, Figs. 13, 14). Aedeagal shaft slender, evenly curved dorsally (Figs. 25, 26) . *plutonis* (Kirkaldy)

— Small species, 2.6–3.1 mm; without the above combination of characters . . . . . . . . . . 8

8(7). Aedeagal shaft slender (Figs. 25, 27) . . . . . . . . . 9

— Aedeagal shaft robust (Figs. 22, 23) . . . . . . . . . 10

9(8). Clypellus with sides straight (Fig. 12). Aedeagal shaft evenly curved throughout length (as in *plutonis*, Fig. 25) . . . . . . . . . *peregrina* (Kirkaldy)

— Clypellus with sides concave. Aedeagal shaft angularly curved basally (Fig. 27) . . . . . . . . . . *usitata* Namba

10(8). Aedeagal shaft sinuate (Fig. 22). Connective elongate, longer than style (Figs. 13, 14) . . . . . . . . . . *timberlakei* (Osborn)

— Aedeagal shaft not sinuate (Fig. 23). Connective approximately equal in length to style . . . . . . . . . . *phoxocephala* Namba

11(1). Female pregenital sternite with disc marked with brown (Fig. 36). Male genitalia as in Figures 37–40 . . . . . . . . . . . . *incisa hospes* (Kirkaldy)

— Female pregenital sternite not marked with brown. Male genitalia as in Figures 41, 42, 45, 46 . . . . . . . . . . . . *saltuella* (Kirschbaum)

## *Balclutha* Kirkaldy

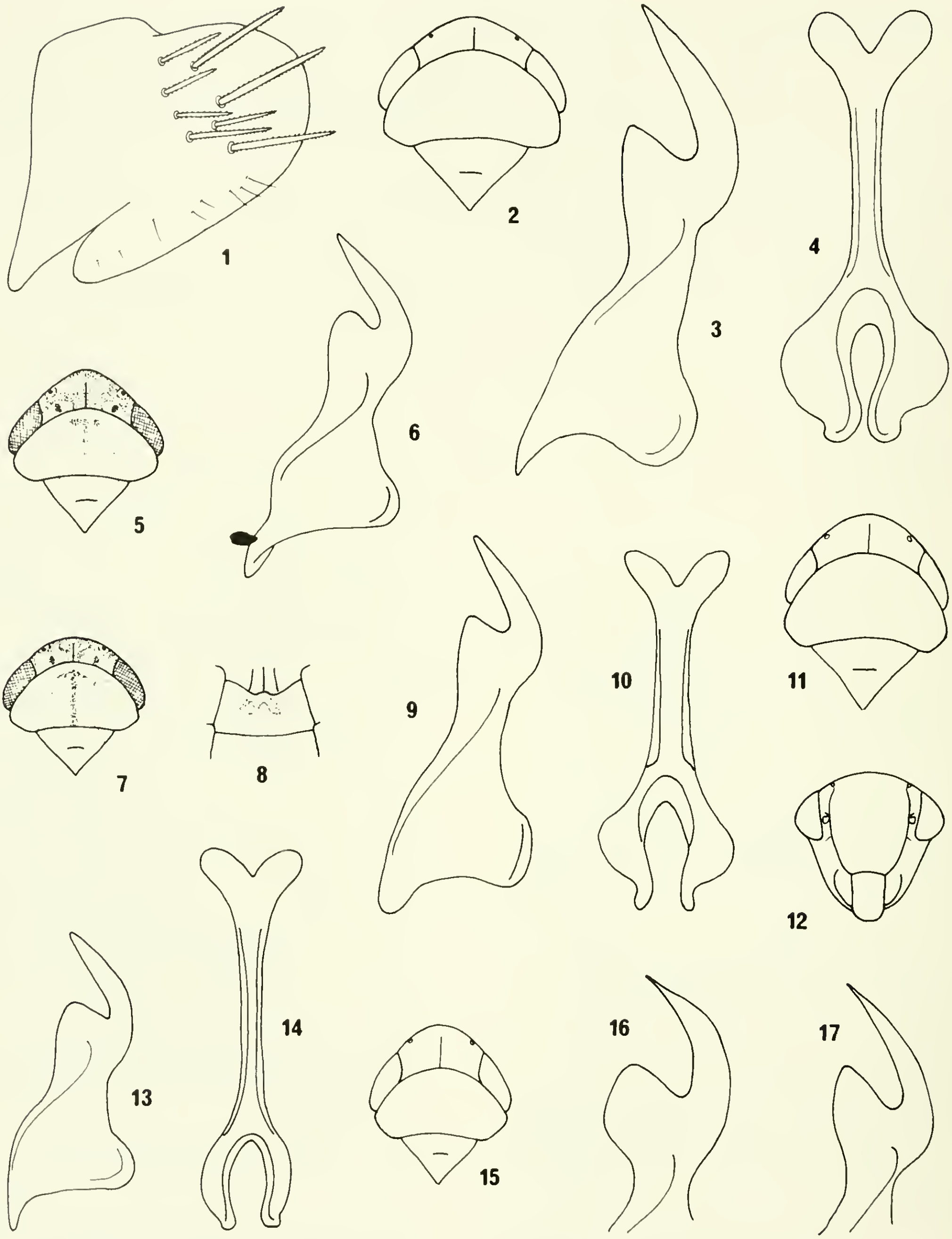
*Balclutha* Kirkaldy, 1900: 243. New name for *Gnathodus* Fieber, 1866; Blocker 1967: 4, Knight 1987: 1178. Type species: *Cicada punctata* Fabricius, 1775, by monotypy.

### *Balclutha fuscifrons*, n. sp.

Figs. 1–4, 18

LENGTH.—♂, 4.0–4.2 mm; ♀, 4.2–4.4 mm. Yellow tinged with green, abdomen heavily marked dorsally and ventrally with dark brown; clypeus pale to dark brown; legs and thoracic sternites variably marked with dark brown.

Head approximately equal in width to pronotum. Vertex with medial length approximately 1.33 times length next to eye. Ocelli marginal, separated from corresponding eye by distance equal to 3–4 times own diameter.




Figs. 1–17. Endemic Hawaiian *Balclutha* species. 1–4, *B. fuscifrons:* 1, male pygofer, left lateral view; 2, head and thorax, dorsal view; 3, right style, dorsal view; 4, connective, dorsal view. 5–7, *B. volcanicola:* 5, head and thorax, dorsal view (Kilauea); 6, right style, dorsal view; 7, head and thorax, dorsal view (Wailua). 8, *B. lobata*, female pregenital sternite. 9–11, *B. nigriventris*: 9, right style, dorsal view; 10, connective, dorsal view; 11, head and thorax, dorsal view. 12, *B. peregrina*, face. 13–15, *B. timberlakei:* 13, right style, dorsal view; 14, connective, dorsal view; 15, head and thorax, dorsal view. 16–17, *B. lobata*, apex of right style, dorsal view.

Face slightly wider than long; clypellus with sides concave, apex extending very slightly beyond margin of face; laterofrontal sutures convex, distally concave, reaching to corresponding ocellus. Setal formulae: foretibia, 1.3 or 1.4; midtibia, 4.3, 4.4, 5.3, or 5.4; hind

femur, 2.1.1 or 2.1.1.1.

MALE.—Pygofer simple, posterior margin broadly and evenly rounded in lateral aspect. Subgenital plate tapered distally to moderately long, fingerlike process. Connective with arms shorter than stem. Style approximately equal in length to connective, preapical lobe elongate. Aedeagal shaft slender, more or less straight distally.

FEMALE.—Pregenital sternite with posterior margin more or less straight. Valvulae as in *incisa* (Figs. 33, 38).

HOST.—Unknown.

DISTRIBUTION.—Endemic (Maui).

HOLOTYPE.—♂, Maui, Kula Pipe Line, 4,200′, vii.1956, R. Namba (BPBM). Paratypes: Maui: 13♂, 19♀, same data as holotype; 4♂, Holua, Haleakala Crater, vi.1983, D. E. Hardy; 4♂, 9♀, Waikamoi, 4,000′, D.E. Hardy (BPBM, BMNH).

REMARKS.—This species can be distinguished by its large size, brown markings, and more or less straight aedeagal shaft. Its external appearance is similar to *Balolina kilaueae*, with which it may be confused.

## *Balclutha volcanicola* (Kirkaldy)

Figs. 5–7, 24

*Nesosteles volcanicola* Kirkaldy, 1910: 574: Osborn 1935: 58, Fig. 24e. Lectotype ♂, Hawaii (BPBM), here designated [examined].

*Balclutha volcanicola* (Kirkaldy): Zimmerman 1948: 87, Fig. 27, Namba 1956: 107–108, Fig. 7.

HOST.—*Cyperus* (Cyperaceae), *Eragrostis* (Gramineae), *Lythrum* (Lythraceae).

DISTRIBUTION.—Endemic (Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Hawaii, Kilauea. Maui: 1♂, Wailua (BPBM). Hawaii: 1♂, paralectotype, same data as lectotype, 1♂, 1 abdomen missing, Kilauea, on *Lythrum* (BPBM); 4♂, Kilauea (BMNH); 4♂, Kealakekua (BMNH).

REMARKS.—This species can be distinguished by its small size (♂, 2.6 mm, ♀, 2.8 mm), stramineous or brown markings on the head (Figs. 5, 7), brown markings on the first thoracic sternite and dorsum of the abdomen, the head being distinctly wider than the pronotum (Figs. 5, 7), 3.3 midtibial setal formula, robust aedeagal shaft (Fig. 24), and the moderately long preapical lobe on the style (Fig. 6).

The medial length of the vertex varies from slightly longer than to 1.5 times length next to eyes (Figs. 5, 7).

## *Balclutha nigriventris*, n. sp.

Figs. 9–11, 19

LENGTH.—♂, 3.0–3.3 mm; ♀, 3.2–3.5 mm.

Yellow to greenish yellow, variably tinged with orange to brown on head, venter, and legs. Dorsum of abdomen dark brown.

External characters as in *fuscifrons*.

MALE.—Genitalia as in *fuscifrons* but with aedeagal shaft curved slightly more dorsally (Fig. 19).

FEMALE.—Genitalia with posterior margin of pregenital sternite more or less straight. Valvulae as in *incisa* (Figs. 33, 38).

HOST.—*Deschampsia* (Gramineae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

HOLOTYPE.—♂, Hawaii: Hualalai, 6,000–7,000′, 21.iv.1944, N. L. H. Krauss (BPBM). Paratypes: Maui: 3♂, 3♀, Halemauu Trail, 1.v.1945, 8,000′ (1♂, on *Deschampsia*); 1♂, Holua, Haleakala Crater, 6,500′, vi.1953. Hawaii: 1♂, 1♀, same data as holotype; 1♀, Hualalai, Hinatapoula, 5,900′, vii.1964 (BPBM, BMNH).

REMARKS.—This species is similar to *fuscifrons* but is significantly smaller, often lacks the brown marking on the clypellus, and has the shaft of the aedeagus slightly different in shape (compare Figs. 18, 19).

## *Balclutha grandis* Namba

Fig. 21

*Balclutha grandis* Namba, 1956: 105–106, Figs. 4a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—Unknown.

DISTRIBUTION.—Endemic (Kauai).

MATERIAL EXAMINED.—Holotype ♂, Kauai: Alakai Swamp, viii.1953, 4,000′ (BPBM).

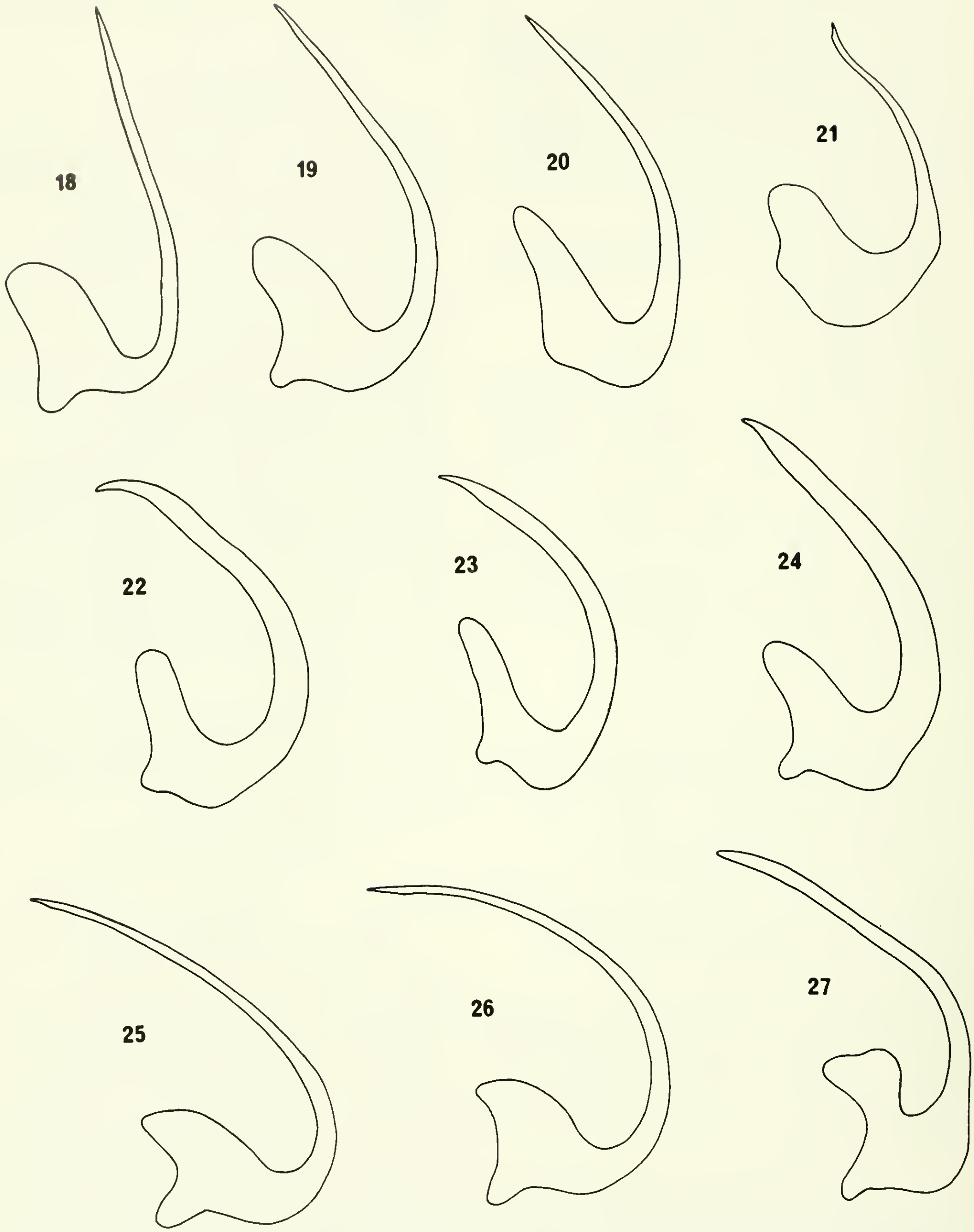
REMARKS.—This species can be distinguished by its large size (♂, 4.5 mm, ♀, 5.3 mm), the head being distinctly wider than the pronotum, 4.4 midtibial setal formula, broad stem of the connective, and the shape of the aedeagus (Fig. 21). Namba (1956) recorded 1♂, 1♀ from the type locality.

## *Balclutha lobata* Namba

Figs. 8, 16, 17, 20

*Balclutha lobata* Namba, 1956: 106, Figs. 5a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes* (Gramineae), *Styphelia* (Epacridaceae).




Figs. 18–27. Endemic Hawaiian *Balclutha* species, aedeagus, left lateral view. 18, *B. fuscifrons;* 19, *B. nigriventris;* 20, *B. lobata;* 21, *B. grandis;* 22, *B. timberlakei;* 23, *B. phoxocephala;* 24, *B. volcanicola;* 25–26, *B. plutonis;* 27, *B. usitata.*

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Kauai, Kokee, vii.1952, 3,600′ (BPBM). Kauai: 8♂, 4♀, Pihea, Kaunuohua Ridge, 4,260′; 6♂, 1♀, Kokee, on *Styphelia*. Molokai: 1♂, Komoku; 9♂, 6♀, above Waikolu V. 1,400m; 1♂, Kalaupapa Lookout; 2♂, Kewala Gulch,

3,500′. Maui: 1♀, Kula Pipe Line, 4, 22′ (BMNH, BPBM).

REMARKS.—This species can be distinguished by its moderately large size (♂, 3.0–3.3 mm, ♀, 3.3–3.4 mm), its dark appearance resulting from the dark brown dorsum of the abdomen and the greenish tinge of the forewings, the 3.3 midtibial setal formula, the disc of the female pregenital sternite marked with brown (Fig. 8), and the large preapical lobe of the style (Fig. 16). Some specimens (Molokai) have the lobe of the style narrower (Fig. 17). Contrary to Namba (1956), the head is approximately equal in width to the pronotum.

*Balclutha plutonis* (Kirkaldy)
Figs. 25, 26

*Nesosteles plutonis* Kirkaldy, 1910: 574: Osborn 1935: 57–58, Fig. 24d. Lectotype ♂, Hawaii, here designated [examined].
*Balclutha plutonis* (Kirkaldy): Zimmerman 1948: 87, Fig. 27, Namba 1956: 105, Fig. 3.

HOST.—*Coprosma* (Rubiaceae), *Vaccinium reticulatus* (Ericaceae), *Sophora* (Leguminosae), *Argyroxiphium virescens*, *Raillardia* (Compositae), *Deschampsia*, *Eragrostis* (?) (Gramineae), *Vincentia* (Cyperaceae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Hawaii, Kilauea, vii.1906, R. C. L. Perkins (BPBM). Numerous specimens from Maui (Haleakala, Puu Luau, Puu Noauiau) and Hawaii (Pohakuloa, Kilauea, Mauna Loa, Hualalai) (BPBM, BMNH).

REMARKS.—This species can be distinguished by its moderately large size (♂, 3.5–3.6 mm, ♀, 3.6–4.0 mm), its uniform yellow or greenish yellow color, usually without brown markings on dorsum of abdomen, and the elongate, evenly curved shaft of the aedeagus. It is similar to *peregrina* but is larger, has the shaft of the aedeagus usually slightly longer, the connective longer than rather than equal in length to the styles, and the sides of the clypellus concave rather than straight. The lectotype is the only specimen known to have the dorsum of the abdomen brown and a slightly shorter aedeagal shaft (Fig. 25), similar to *peregrina*. The setal formulae vary as follows: foretibia, 1.3, 1.4, or 1.5; midtibia, 4.4 or 5.4; hind femur, 2.1.1 or 2.1.1.1.

*Balclutha peregrina* (Kirkaldy)
Fig. 12

*Nesosteles peregrina* Kirkaldy, 1910: 575. Holotype ♂, Hawaii (BPBM) [examined].
*Balclutha peregrina* (Kirkaldy): Zimmerman 1948: 86–87, Fig. 27, Namba 1956: 108, Figs. 8a–c.

HOST.—*Cyathodes*, *Deschampsia* (Gramineae), *Railliardia* (Compositae), *Vaccinium* (Ericaceae), *Styphelia* (Epacridaceae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Hawaii: Kilauea, vi.1903, R.C.L.P. Hawaii: (numerous specimens from Kilauea); 2♂, 5♀, Stainback Highway, 2,134 m, on *Styphelia* (BPBM, BMNH).

REMARKS.—This species is similar to *plutonis* but is significantly smaller (♂, 2.6–3.1 mm; ♀, 2.8–3.1 mm), has the abdomen sometimes marked with pale brown, the sides of the clypellus straight (Fig. 12), and the midtibial setal formula 4.3 or 4.4. A few specimens examined (Stainback Highway) are tinged with scarlet and have the abdomen and thoracic sternites marked with dark brown.

*Balclutha usitata* Namba
Fig. 27

*Balclutha usitata* Namba, 1956: 104–105, Figs. 2a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Kauai, Kainamanu, vii.1952, 3,800′ (BPBM). Numerous specimens from throughout its range (BMNH, BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 2.6–2.9 mm, ♀, 2.8–3.1 mm), its overall yellow or greenish yellow color without brown markings on the dorsum of the abdomen, the 3.3 midtibial setal formula, and the angularly curved aedeagal shaft (Fig. 27). Some specimens have stramineous markings similar to but paler than in *volcanicola* (Figs. 5, 7).

*Balclutha timberlakei* (Osborn)
Figs. 13–15, 22

*Nesosteles timberlakei* Osborn, 1935: 59–60, Figs. 25a–d. Holotype ♂, Oahu (BPBM) [examined].
*Balclutha timberlakei* (Osborn): Zimmerman 1948: 87, Figs. 7e, 24c; Namba 1956: 108–109, Figs. 9a–b.

HOST.—*Eragrostis variabilis* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu,

Molokai, Lanai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Oahu (BPBM). Oahu: 1♂ (paratype) Palolo Val. on *Eragrostis variabilis* (BMNH). Maui: 1♂, Waikapu Val. (BPBM). Hawaii: 1♂, 2♀, Pohakuloa, 1,800 m (BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 3.0 mm, ♀, 3.4 mm), elongate head that is distinctly wider than the pronotum (Fig. 15), general yellow color without brown markings on the dorsum of the abdomen, 3.3 midtibial setal formula, robust and slightly sinuate shaft of the aedeagus (Fig. 22), and its elongate connective, which is longer than the style (Figs. 13, 14).

*Balclutha phoxocephala* Namba
Fig. 23

*Balclutha phoxocephala* Namba, 1956: 109, Fig. 10. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes*, *Eragrostis variabilis* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai).

MATERIAL EXAMINED.—Holotype ♂, Kauai: Nualolo, viii.1925, on *Cyathodes* (BPBM). Kauai, Oahu, Molokai (9♂, 5♀, paratypes, BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 2.4–2.6 mm, ♀, 2.7–3.0 mm), 3.3 midtibial setal formula, and robust aedeagus (Fig. 23). Some specimens have stramineous markings similar to but paler than in *volcanicola*.

A series of specimens from Hawaii, Pohakuloa, 6,300′ (BPBM), may be this species but have the aedeagal shaft more robust.

*Balclutha incisa hospes* (Kirkaldy), n. stat.
Figs. 28–40

*Nesosteles hebe* var. *hospes*, Kirkaldy, 1910: 574; Osborn 1935: 57, Figs. 24a–b. Lectotype ♀, Hawaii (BPBM), designated by Zimmerman (1948: 85) [examined].

*Nesosteles hospes* Timberlake, 1918: 381.

*Balclutha hospes* (Kirkaldy): Zimmerman, 1948: 85, Fig. 24b, Namba 1956: 107, Figs. 6a–b.

HOST.—*Chloris radiata*, *Panicum purpurascens* (Gramineae).

DISTRIBUTION.—Cosmopolitan and throughout the Hawaiian islands.

MATERIAL EXAMINED.—Lectotype ♀ of *Nesosteles hebe* var. *hospes*, Hawaii: Kauai (BPBM). Numerous specimens from Kauai, Oahu, Molokai, and Hawaii (BPBM, BMNH).

REMARKS.—This subspecies can be distinguished by the head being slightly wider than the pronotum, the short vertex (Fig. 28), the ocelli being only 1.0–1.5 times their own diameter from the corresponding eye, the coronal suture visible in facial view (Fig. 29), distinctively shaped aedeagus (Figs. 39, 40), and the brown markings on the female pregenital sternite (Fig. 36). It is similar in external appearance to *B. saltuella* (see REMARKS under *saltuella*).

This subspecies, which occurs in Hawaii, the Marquesas Islands, and the Americas, differs from the nominate subspecies in the Old World by the more laterally directed ventral process of the aedeagus. This distinction suggests that the species may have reached Hawaii from the Americas rather than the Pacific. Contrary to Timberlake's data (1918), the shape of the pygofer process (Fig. 37) is similar but variable in both subspecies.

*Balclutha saltuella* (Kirschbaum)
Figs. 41–46

*Jassus (Thamnotettix) saltuellus* Kirschbaum, 1868; 86. Holotype ♀, Germany (Museum Wiesbaden) [examined].

*Balclutha beardsleyi* Namba, 1956: 110, 112, Figs. 11a–b. Holotype ♂, Hawaii (BPBM) [examined], syn. nov.

HOST.—Unknown in Hawaii; elsewhere: *Agrostis* (Gramineae) and *Gossypium* (Malvaceae) (Knight 1987).

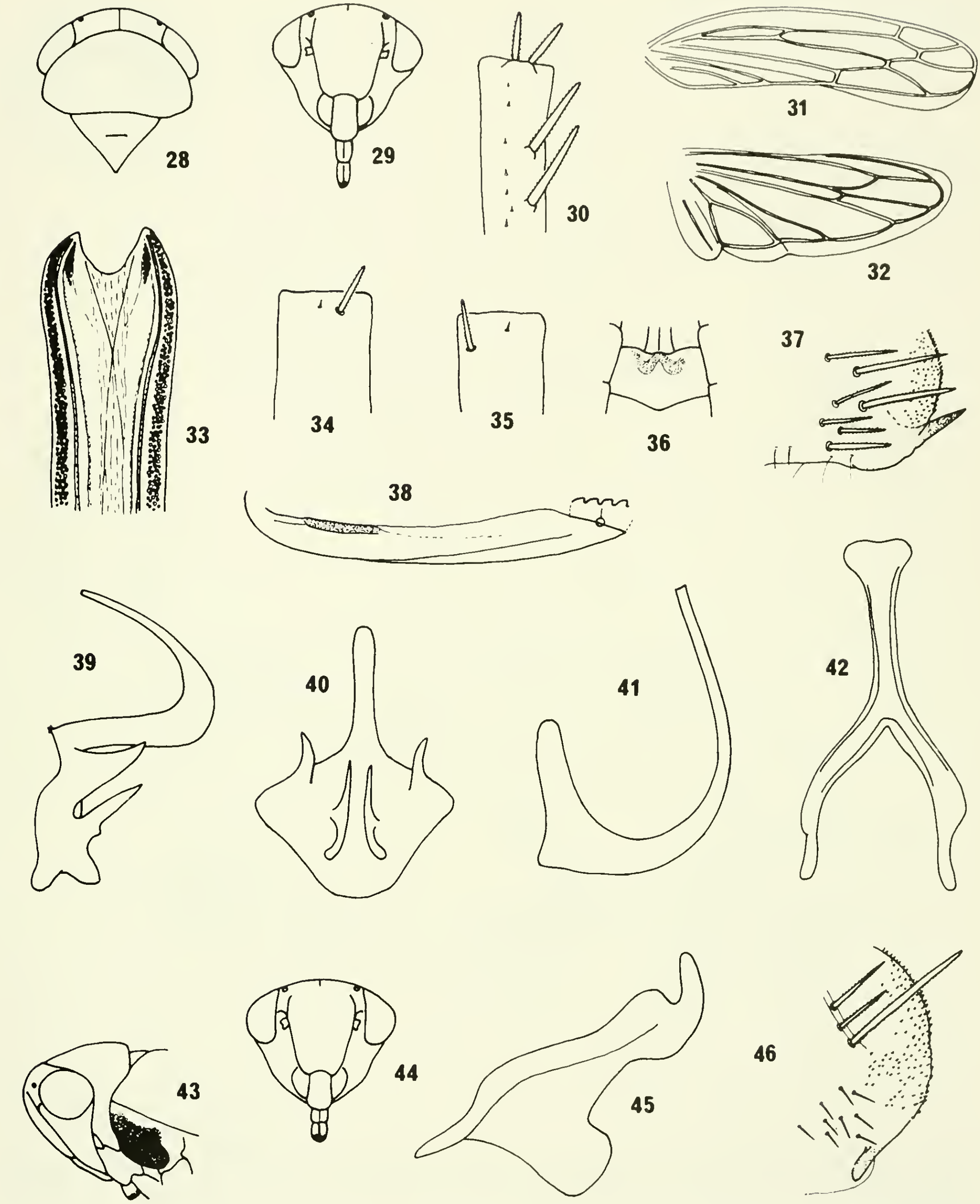
DISTRIBUTION.—Cosmopolitan and on Oahu.

MATERIAL EXAMINED.—Holotype ♀ *Jassus (Thamnotettix) saltuellus*, Germany (Museum Wiesbaden). Holotype ♂ *B. beardsleyi*, Oahu: Honolulu, i.1955 (BPBM). Oahu: 1♂, 3♀, Honolulu; 1♀, Ewa (BPBM).

REMARKS.—This species is similar to *B. incisa* in external appearance but differs from this and other Hawaiian species by its reduced number of foretibial spines (1.1), its medially directed, lateral frontal sutures, and the short, broad rostrum in facial view (Fig. 44). It differs from *incisa*, in addition, by having the prosternum dark brown (Fig. 43), the female pregenital sternite with a medial, triangular lobe on the posterior margin, and the disc devoid of brown markings.

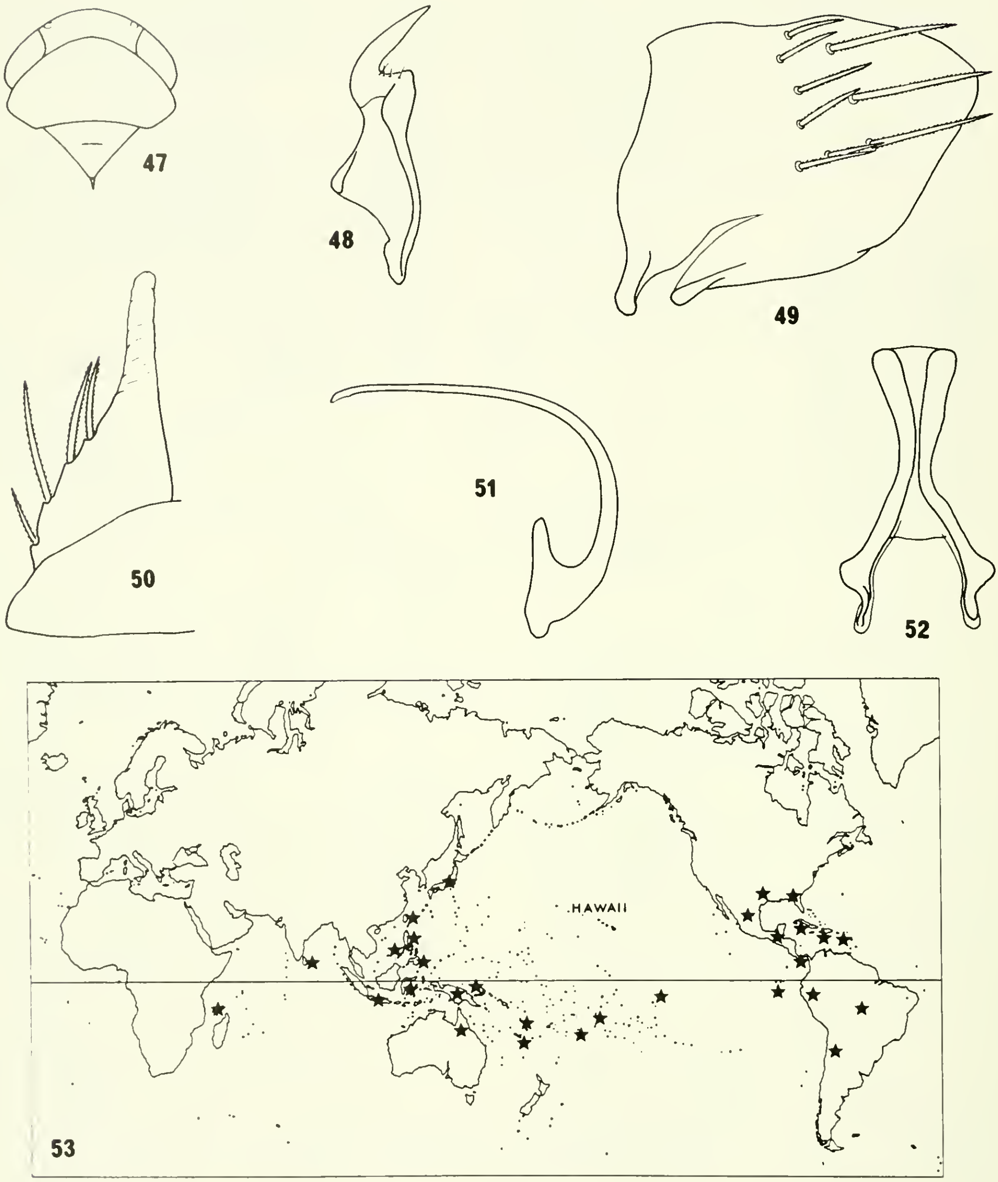
*Nesolina* Osborn

*Nesolina* Osborn, 1935: 60. Type species: *Nesolina lineata* Osborn, by original designation: Zimmerman 1948: 87.




Figs. 28–46. *Balclutha* species. 28–40, *B. incisa hospes:* 28, head and thorax, dorsal view; 29, face; 30, apex of left hind femur; 31, right forewing; 32, right hindwing; 33, apex of second valvulae, ventral view; 34, apex of left midtibia; 35, apex of left foretibia; 36, female pregenital sternite; 37, ventroposterior corner of male pygofer lobe, lateral view; 38, left second valvula, lateral view (toothed area between broken lines); 39, aedeagus, left lateral view; 40, aedeagus, posterior view. 41–46, *B. saltuella:* 41, aedeagus, left lateral view; 42, connective, dorsal view; 43, head and thorax, left lateral view; 44, face; 45, right style, dorsal view; 46, posteroventral corner of male pygofer lobe.

REMARKS.—This endemic Hawaiian genus can be distinguished by its long head and distinctive markings, its large aedeagus without processes, and the plumose macrosetae of



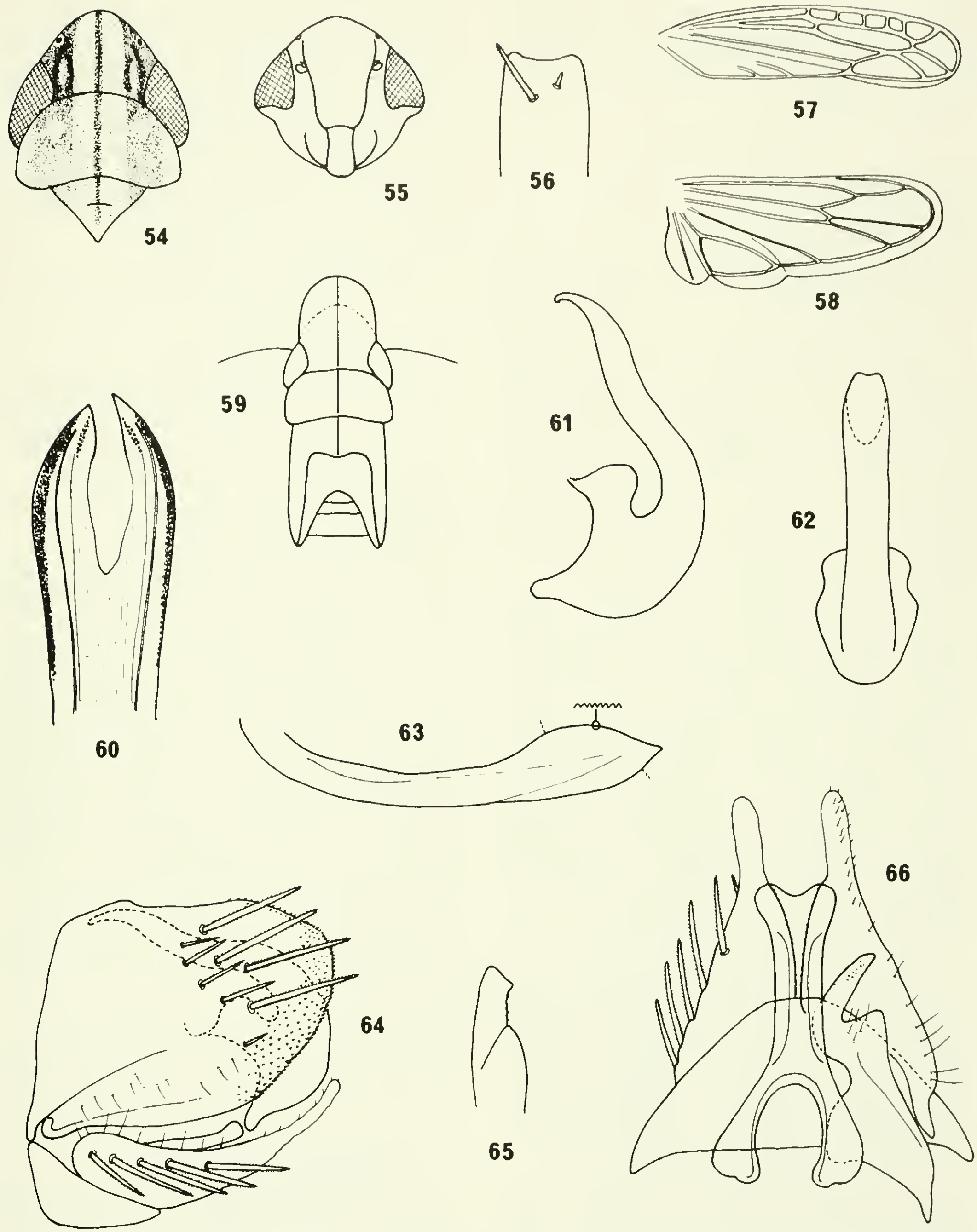

Figs. 47–53. *Balclutha lucida:* 47, head and thorax, dorsal view; 48, left style, dorsal view; 49, male pygofer, left lateral view; 50, left subgenital plate, ventral view; 51, aedeagus, left lateral view; 52, connective, dorsal view; 53, distribution.

the legs and genitalia. The foretibia and midtibia each have one long, and one short, stout apical seta. Setal formulae: foretibia, 1.3; midtibia, 3.3; hind femur, 2.1.1. (see also REMARKS under "Relationship of *Balclutha* to Other Hawaiian Macrostelini").

## *Nesolina lineata* Osborn

Figs. 54–66

*Nesolina lineata* Osborn, 1935: 60–61, Figs. 26a–c: Zimmerman 1948: 88, Figs. 7d, 8e–f, 24d. Lectotype ♂, Oahu (BPBM), here designated [examined].




Figs. 54–66. *Nesolina lineata:* 54, head and thorax, dorsal view; 55, face; 56, apex of left foretibia; 57, right forewing; 58, right hindwing; 59, immature, head and thorax, dorsal view; 60, apex of first valvulae; 61, aedeagus, left lateral view; 62, aedeagus, posterior view; 63, left second valvula, lateral view (toothed area between broken lines); 64, male genital segment, left lateral view; 65, apex of left style, lateral view; 66, subgenital plates, dorsal and ventral view, valve, connective, and left style, dorsal view.

HOST.—*Eragrostis variabilis* (Gramineae).
DISTRIBUTION.—Endemic (Oahu, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Oahu: Diamond Head, 18.ii.1917, W. M. Giffard.

Oahu: 11♂, 8♀, 5 immatures, Diamond Head, various dates (paralectotypes) (BPBM). Hawaii: 1♂, Kau; 1♂, Pohakuloa, on bunch grass (BMNH).

### *Balolina*, n. gen.

Type species: *Macrosteles kilaueae* Kirkaldy.

LENGTH.—3.6–4.3 mm.

Yellow to greenish yellow, variably marked with brown. Head slightly to distinctly narrower than pronotum. Vertex triangular, medial length approximately 1.5 times length next to eye, foremargin broad to narrowly parabolic. Ocelli marginal, visible dorsally, situated approximately midway between eye and midline. Face slightly wider than long, lateral margin strongly sinuate below eye. Clypeus narrow, lateral margins incurved at level of eye. Transclypeal suture indistinct. Clypellus narrow, slightly expanded to near apex, extended well beyond margin of face. Laterofrontal sutures extending one-half distance to corresponding ocellus. Pronotum 1.5 times length of vertex, lateral margins short. Forewings elongate, appendix wide, extending around first and second apical cells; outer subapical cell absent; inner subapical cell open basally. Hindwing with veins r and m fused distally. Forefemora with two stout apical setae. Foretibia setal formula 1.3. Midfemora with one long, and one moderately long, stout apical seta. Midtibia setal formula usually 3.3. Hind femora setal formula usually 2.2.1. Base of hind tarsomere sulcate.

MALE.—Pygofer narrowly rounded posteriorly; a group of submarginal macrosetae posteriorly. Subgenital plates gradually tapered to lightly sclerotized, fingerlike apex; a multiseriate row of macrosetae along ventrolateral margin. Styles with apical process tapered to acute apex in ventral view, apex footlike in medial view; lateral lobe well developed; inner basal apophyses short. Connective Y-shaped; stem short, equal in length to arms; articulating with aedeagus. Aedeagus with shaft short and robust, cylindrical; a pair of short processes apically; gonopore apical on ventral surface; basal apodeme short.

FEMALE.—First valvulae fused. Second valvulae evenly tapered to acute apex; teeth very fine, extending over distal half of dorsal margin and onto apex of ventral margin.

REMARKS.—This genus is similar in appearance to *Balclutha* and *Nesoclutha* but can be distinguished from these genera by the absence of hairy macrosetae, shorter laterofrontal sutures, indistinct transclypeal suture, the ocelli situated more distant from the eyes, the subgenital plates with multiseriate macrosetae, and the aedeagus with a pair of apical processes. It differs from *Balclutha* also by the other characters noted in the key.

### *Balolina kilaueae* (Kirkaldy), n. comb.

Figs. 67–83

*Macrosteles kilaueae* Kirkaldy, 1910: 575. Holotype ♀, Hawaii (BPBM) [examined].

*Balclutha kilaueae* (Kirkaldy): Zimmerman 1948: 86, Figs. 7a, 11d–f; Namba 1956: 103–104, Figs. 1a–b.

HOST.—*Cibotium chamissoi* and *C. menziesii* (Dicksoniaceae) (ferns).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♀, Hawaii, Kilauea, vii.1906, RCL Perkins. Numerous specimens from throughout its range (BPBM, BMNH).

REMARKS.—The specimens examined varied in color and in the length of the vertex. Brown markings are often present on the dorsal and ventral surfaces of the abdomen and sometimes on the thorax, the clypeus, the basal two-thirds of the ovipositor, the basal half of the corium of the forewing, and the hind legs. One specimen examined from Maunawainui Valley, Molokai, has the clavus of the forewing pale scarlet. Setal formulae: foretibia, 1.3; midtibia, usually 3.3 but sometimes 4.3, 4.4, or 5.3; hind femur, usually 2.2.1, sometimes 2.1.1.1, 2.2.1.1, or 2.1.2.1.1.

This species is similar in external appearance to *Balclutha nambai* with which it may be confused.

## ACKNOWLEDGMENTS

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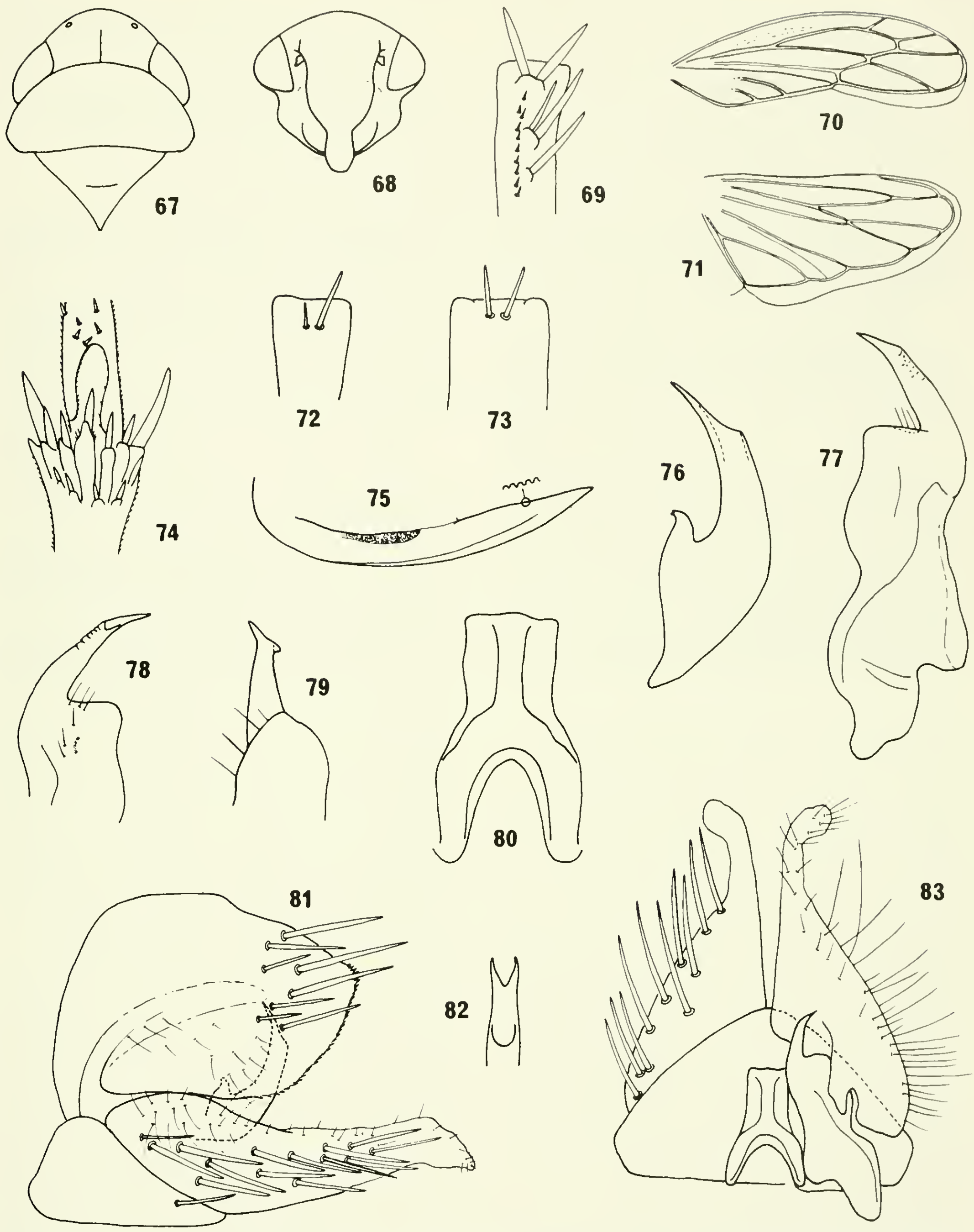


Figs. 67–83. *Balolina kilaueae:* 67, head and thorax, dorsal view; 68, face; 69, apex of left femur; 70, right forewing; 71, right hindwing; 72, apex of left midtibia; 73, apex of left foretibia; 74, apex of hind tibia and base of first tarsus; 75, left second valvula, lateral view (toothed area between broken lines); 76, aedeagus, left lateral view; 77, right style, dorsal view; 78–79, apex of right style, ventral and medial view; 80, connective, dorsal view; 81, male genital segment, left lateral view; 82, apex of aedeagus, posterior view; 83, subgenital plates, dorsal and ventral view, valve, connective, and left style, dorsal view.

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# *COLLADONUS* AND RELATED GENERA OF MEXICO AND CENTRAL AMERICA WITH NEW TAXA AND SYNONYMY (HOMOPTERA: CICADELLIDAE)

M. W. Nielson[1]

ABSTRACT.—A study of the genus *Colladonus* and related genera of Mexico and Central America was based almost exclusively upon the examination of nearly the entire type series of all the *Idiodonus* species described by the late Dr. D. M. DeLong. All species referable to *Colladonus* are redescribed, and illustrations of the male genitalia are given for the first time. A key to the species of Mexico and Central America is also included. A brief discussion of the distribution and phylogeny of the group is given.

Among 35 species described by DeLong in *Idiodonus*, 21 belong in *Colladonus*, 1 is assigned to *Ollarianus* Ball, 1 to *Paratanus* Young, 2 to *Bonneyana* Oman, 2 are retained in *Idiodonus*, 5 are relegated to four proposed new genera, and the remaining 3 have uncertain generic position. One new combination in *Colladonus* is proposed, and 16 names are treated as new synonyms. Eight new combinations are proposed in the treatment of related genera. New genera include: *Paracolladonus*, *Paracrassana*, *Paranurenus*, and *Jaacunga*. The subgenus *Angulanus* DeLong is elevated to generic rank.

The genus *Colladonus* Ball was first revised by Nielson (1957), who treated primarily the Nearctic species north of Mexico and one known single Palearctic species. After the major part of the revisionary work was finished, a number of Mexican leafhoppers described by DeLong (1946) in the genus *Idiodonus* Ball were studied, and several species were found referable to *Colladonus*. Twelve species were listed as new combinations and treated as *incertae sedis* in the appendix of my 1957 paper. Two species-level names were suppressed as new synonyms of an older name. Time did not permit a more thorough study of suspected additional synonymy and possible dissociation of the sexes between the female holotype and male allotype of several species in this group.

The descriptions of nearly all of DeLong's *Idiodonus* species were based on females, and a female specimen was designated as the holotype in nearly all cases. Illustrations were limited to a dorsal view of the head and thorax, and a ventral view of the female seventh sternum, which with color patterns formed the basis of his classification. In a much later paper, DeLong (1983) described additional species of *Idiodonus* from Mexico and Bolivia; then he (DeLong 1984) prepared a revised key to all the known species in the New World, separating them on the basis of color patterns and configuration of the female seventh sternum.

Although the female seventh sternum alone is a useful character for separating some species of *Colladonus*, its utility is enhanced only in combination with male genital characters. This is particularly true in certain species that show similarities in male characters that require support by associated female seventh sternal characters to differentiate these species.

In this study the entire type series, with the exception of a few specimens, of all species of *Idiodonus* described by DeLong were examined with attention given to association of the female holotype and her counterpart male allotype or male paratype specimen. A few cases of improper sex association were found, and these are discussed below. All species found referable to *Colladonus* are redescribed, and illustrations of the male genitalia are given for the first time. A key to the species of Mexico and Central America is also included. Six new species of *Colladonus* are described from that region. One new combination is proposed, those treated as new combinations in my earlier paper are confirmed, and 16 names are treated as new synonyms under their respective nominate species-level name. *Colladonus delongi* described by Linnavuori (1959) from Panama and based on an apparent mislabeled and misdetermined female specimen was treated as a new synonym of *Colladonus montanus* (Van Duzee) by Nielson (1966).

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Among 35 species described in *Idiodonus* by DeLong, 21 belong in *Colladonus* (including 14 species treated in my earlier work), 1 is assigned to *Ollarianus* Ball, 1 to *Paratanus* Young, 2 to *Bonneyana* Oman, 2 are retained in *Idiodonus*, 5 are relegated to four proposed new genera, and the remaining 3 have uncertain generic position. One species, *I. plummeri* DeLong, is considered the only valid and correctly placed species among all those described in *Idiodonus* by DeLong. *Idiodonus bakeri* DeLong is suppressed as a new synonym of *plummeri*. DeLong treated 6 older species of *Idiodonus* in his 1946 paper, 5 of which were subsequently assigned to three other genera by Oman (1949). Descriptions of four new genera, *Paracolladonus*, *Paracrassana*, *Paranurenus*, and *Jaacunga*, are provided with redescriptions and illustrations of the species assigned to their respective genus. The subgenus *Angulanus* DeLong is elevated to generic rank.

DISTRIBUTION OF *COLLADONUS*.—The origin of the genus appears to have been centered in the southern highland range of the Nearctic region (Rocky Mountain subregion) in Mexico where radiation northward produced the bulk of species in United States. Only one species is known to occur as far south as Panama, and one is widespread in the Palearctic region. Fifteen species occur in Mexico proper, only one of which ranges into Arizona. Among 44 species in United States (including Alaska) and Canada, seven occur marginally in Mexico (Bliven 1954, Nielson 1962, 1966). Most of the species of *Colladonus* occur on trees and shrubs in the mountainous regions of western United States and Canada.

Genera closely allied to *Colladonus* (*Nigridonus* Oman, *Caladonus* Oman, *Bonneyana* Oman, and two new genera) are known only from Mexico and the extreme southwestern mountain areas of the United States, lending support to the Mexican origin of the genus *Colladonus*.

With respect to the New World distribution of *Idiodonus*, it is doubtful that the genus occurs south of Mexico. Members of the genus are more common in the United States than in Mexico.

CONSIDERATIONS OF PHYLOGENY.—Nearly all female *Colladonus* of species that occur north of Mexico have a spatulate process on the caudal margin of the seventh sternum. None of the species in Mexico and Central America possess this structure, suggesting that it is a derived (apomorphic) character. The spatulate process thus far has attained its highest development in *C. furculatus* (Osborn) that occurs in the eastern United States and Canada. There does not appear to be any correlation between the presence of this structure and male genital structures, indicating that its development was independent of the evolutionary development in male structures. However, there appears to be a correlation between the absence of the spatulate process on the female seventh sternum and a short, male pygofer spine among the species (United States, Canada, and Palearctic region) that possess these characters, viz., *belli*, *youngi*, *brunneus*, and *torneellus*. This relationship does not hold true for species in Mexico and Central America, suggesting that the northern population evolved separately from its sister population in the United States and Canada that does not exhibit this relationship.

About half of the *Colladonus* species have crowns that are produced, which is considered a more primitive condition. Associated with this character is the relative position of the gonopore on the shaft of the aedeagus. A gonopore basad of the midlength of the aedeagal shaft is considered more primitive, whereas a position distad of middle is more advanced. About 82% of the United States and Canadian species bearing a basal gonopore have a produced crown, whereas all of those species bearing a distal gonopore have a short, rounded crown. Among the Mexican and Central American species, nearly all species with a basal gonopore have a produced crown, whereas all species with a distal gonopore have a short, rounded crown. Each of those sister groups apparently evolved independently.

Key to Males of *Colladonus* of Mexico and Central America

| | | |
|---|---|---|
| 1. | Pronotum with yellow or ivory, (sometimes pale) *transverse* band | 2 |
| — | Pronotum without such band | 13 |
| 2(1). | Pygofer with a very short, exposed spine on caudal margin, exposed length about twice as great as exposed basal width | 3 |
| — | Pygofer with moderately long to very long, exposed spine on caudal margin, exposed length nearly three times to more than five times as great as exposed basal width | 8 |

3(2). Pygofer spine near middle of caudal margin; connective short, not reaching to apex of style; aedeagus with bifurcated processes long, reaching to midlength of shaft . . . . . . . . . 4

— Pygofer spine distinctly basad of middle of caudal margin; connective long, reaching to apex of style; aedeagus with bifurcated processes short, not reaching to midlength of shaft . . . . . . . . . . . . . . . . . *albocinctus* (DeLong)

4(3). Pygofer spine near middle or just below middle of caudal margin . . . . . . . . . . . . . . . . . . . . 5

— Pygofer spine distinctly above middle of caudal margin . . . . . . . . . . . . . . . . . . . . *belli* (Uhler)

5(4). Pygofer with caudoventral margin smooth; style with apical stylar spine . . . . . . . . . . . . . . . 6

— Pygofer with caudoventral margin toothed or serrate; style with subapical stylar spine . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *serratus*, n. sp.

6(5). Aedeagus with bifurcated processes long, extending beyond gonopore in lateral view . . . . 7

— Aedeagus with bifurcated processes short, not reaching to gonopore in lateral view . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *fasciaticollis* (Stal)

7(6). Style with apical shaft broad and lateral margins parallel, stylar spine apical and projecting laterad . . . . . . . . . . . . . . . . . . *ultimus*, n. sp.

— Style with apical shaft narrowed distally, lateral margins not parallel, stylar spine apical and projecting laterodistad . . . *tolucensis*, n. sp.

8(2). Pygofer spine with exposed length not more than 4 times exposed basal width . . . . . . . . . . . 9

— Pygofer spine with exposed length more than 5 times exposed basal width . . . . . . . . . . . . . . 11

9(8). Connective short, not reaching to apex of style; aedeagus in lateral view with bifurcated process short, reaching to about midlength of shaft . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

— Connective long, reaching to about apex of style; aedeagus in lateral view with bifurcated processes long, extending beyond midlength of shaft . . . . . . . . . . . . . . . . . . *dampfi* (DeLong)

10(9). Pronotum with narrow, black band on anterior margin and narrow, black, transverse band on middle; style with lateral margins of distal shaft smooth . . . . . . . . *bicinctus* (DeLong)

— Pronotum with narrow, black band on anterior margin but without medial, black, transverse band; style with inner lateral margin of distal shaft toothed . . . . . . . *claustrus* (DeLong)

11(8). Pygofer with caudoventral margin and pygofer spine smooth, without serrations or teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

— Pygofer with caudoventral margin serrate or toothed, pygofer spine toothed basally . . . . . . . . . . . . . . . . . . . . . . . . . . . . *verecundus* (DeLong)

12(11). Pygofer with spine arising about middle of nearly truncate caudal margin; connective very long, extending beyond apex of style; aedeagus with bifurcated processes short, nearly reaching to midlength of shaft . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *titulus* (DeLong)

— Pygofer with spine arising from apex of distally produced caudoventral margin; connective short, extending nearly to apex of style; aedeagus with bifurcated processes long, extending beyond midlength of shaft . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *singularius*, n. sp.

13(1). Pronotum never with yellow, longitudinal band; claval veins not deeply marked with yellow, if yellow, very pale or ivory . . . . . . . . 14

— Pronotum with yellow, *longitudinal* band, claval veins deeply marked with yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *trabilis*, n. sp.

14(13). Pygofer spine very long, exposed length more than 5 times exposed basal width . . . . . . . . . . 15

— Pygofer spine short, exposed length not more than 3 times exposed basal width . . . . . . . . . . 16

15(14). Crown with two handlebar-shaped markings on anterior margin; aedeagus with very long, reflexed, bifurcated processes in lateral view, processes parallel in dorsal view . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *clathrus* (DeLong)

— Crown with as many as 8 black spots on anterior margin, some spots sometimes connected, if so, never handlebar shaped; aedeagus with short bifurcated processes nearly reaching midlength of shaft in lateral view, processes crossing over in dorsal view . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *beameri* (Ball)

16(14). Pygofer with caudal margin smooth . . . . . . . . 17

— Pygofer with caudal margin serrate or toothed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

17(16). Pygofer with very short spine arising from caudoventral margin; aedeagus with gonopore at about middle of shaft; connective long, reaching to about apex of style . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *albocinctus* (DeLong)

— Pygofer with moderately long spine arising from middle of caudal margin; aedeagus with gonopore basad of middle shaft; connective short, not reaching apex of style . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tessellatus*, n. sp.

18(16). Pygofer with caudoventral margin produced distally, small, robust spine arising from caudodorsal angle, projecting dorsally; style with distal shaft long and narrow, serrate on inner lateral margin; aedeagus with gonopore at middle of shaft. . . . . . . . . . *anademus* (DeLong)

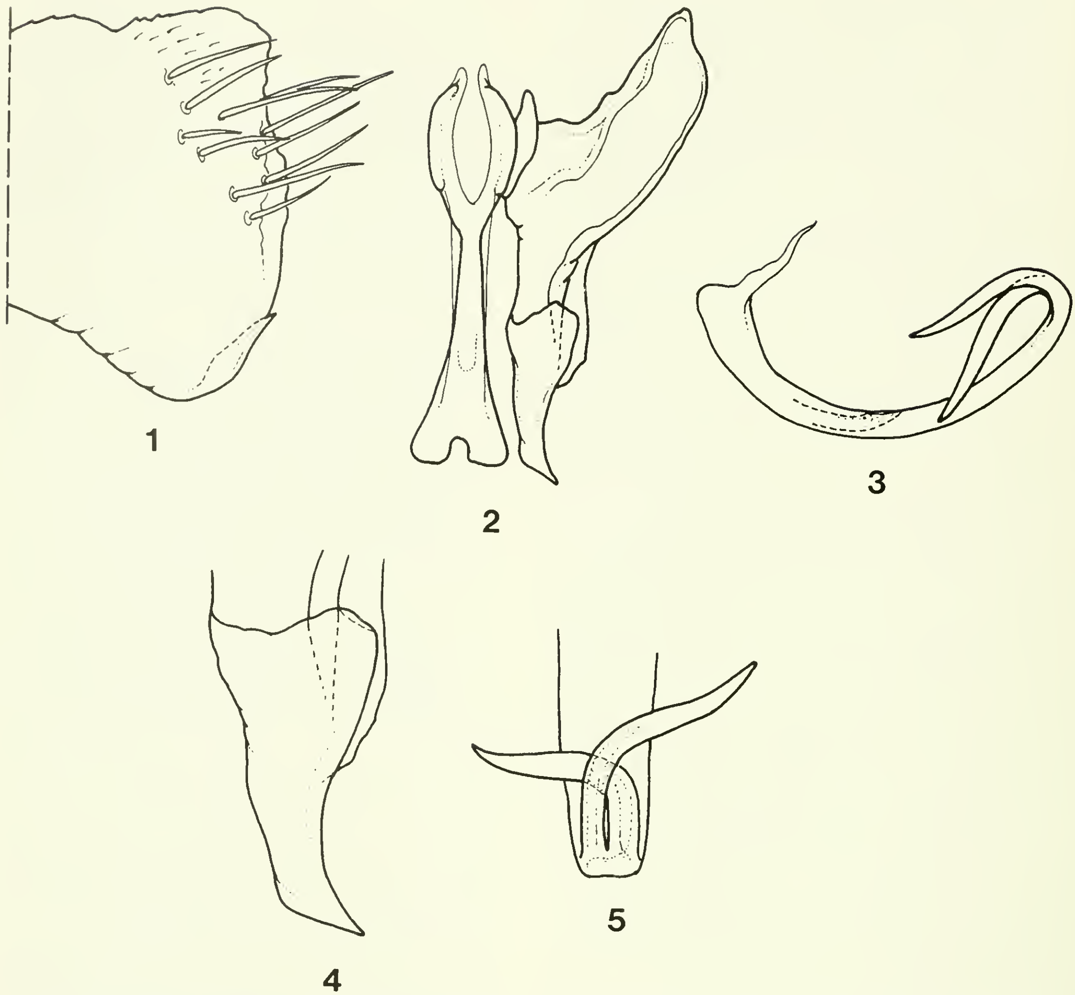
— Pygofer with obtusely angled caudal margin, very small spine arising from apex of angle and projecting distad; style with distal shaft robust and short, smooth on inner lateral margin; aedeagus with gonopore basad of middle of shaft . . . . . . . . . . . . . . . . . . . . *incidus* (DeLong)

## *Colladonus albocinctus* (DeLong)

Figs. 1–5

*Idiodonus albocinctus* DeLong 1946:22 [Holotype ♀ (OSU) (examined).]

*Colladonus albocinctus:* Nielson 1957:51




Figs. 1–5. *Colladonus albocinctus* (DeLong): 1, male pygofer, lateral view; 2, connective and right style, dorsal view; 3, aedeagus, lateral view; 4, apex of right style, enlarged dorsal view; 5, apex of aedeagus and distal processes, enlarged dorsal view.

*Idiodonus albocinctus:* Metcalf 1967:1286
*Idiodonus albocinctus:* DeLong 1984:10
*Idiodonus nigridens* DeLong 1946:29 [Holotype ♀ (OSU) (examined).] New synonymy
*Colladonus nigridens:* Nielson 1957:51
*Idiodonus nigridens:* Metcalf 1967:1301
*Idiodonus nigridens:* DeLong 1984:10
*Idiodonus sexpunctatus* DeLong 1983:90 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus sexpunctatus:* DeLong 1984:10

LENGTH.—Male, 4.9–5.0 mm; female, 5.0–5.3 mm.

Color variable from absence to presence of narrow, ivory, transverse band about middle of pronotum, with two black spots on anterior margin of crown and absence or presence of narrow, black, transverse band on disc of crown. Similar in general habitus to *verecundus* (DeLong) and in male genitalic characters to *fasciaticollis* (Stal).

Head with anterior margin produced, apex obtusely angulate.

MALE.—Pygofer in lateral view with very short, exposed caudoventral spine arising below middle of caudal margin, basal nine-tenths of spine sclerotized and fused to pygofer wall (Fig. 1); aedeagus in lateral view with bifurcated distal processes less than half as long as aedeagal shaft, not reaching gonopore (Fig. 3), crossing over in dorsal view (Fig. 5), gonopore at about midlength of shaft;

connective long, extending to about apex of style (Fig. 2); style with distal shaft broad, lateral margins smooth, stylar spine broad and bluntly pointed, projecting laterodistally (Fig. 4).

FEMALE.—Seventh sternum produced distally to form broad medial lobe, with median, shallow notch on its caudal margin, configuration of lobe variable, sometimes with small lobe at base of notch.

DISTRIBUTION.—This species has been collected in the Mexican states of Distrito Federal, Michoacán, Morelos, and Hidalgo.

HOST.—Some specimens were collected in pine forests at elevations of 7,500 feet from July to October (DeLong 1946).

REMARKS.—The configuration of the female seventh sterna of the holotypes of *nigridens* and *sexpunctatus* is similar, with some intra- and interpopulation variation in the angle of the posteriolateral margins. The abdomen of the female holotype of *albocinctus* is missing, but comparisons were made with paratype female specimens after they were associated with holotype and with DeLong's illustration of the seventh sternum. Although the male genital structures of the allotypes of *albocinctus* and *nigridens* are nearly identical, the latter is more deeply sclerotized than the former. The sexes of both species appear to be properly associated.

The female holotype of *sexpunctatus* is identical in general habitus with the female holotype of *nigridens*, but both species differ markedly in color patterns from *albocinctus*. The latter species has a distinctive pronotal band that is absent in the specimens of the two former species. The male genital structures, however, are identical among these populations, which suggests that two infraspecific entities may be involved. Such action is deferred until more material is collected and studied.

*Colladonus albocinctus* is distinguished from *fasciaticollis* by the position of the pygofer spine, which is distinctly basad of the middle of the caudal margin of the pygofer.

## *Colladonus belli* (Uhler)

Figs. 6–10

*Jassus belli* Uhler 1877:471 [Holotype ♀ (USNM) (examined).]
*Thamnotettix belli:* Van Duzee 1892:306
*Colladonus belli:* Ball 1936:58
*Idiodonus belli:* Medler 1943:18
*Colladonus belli:* Nielson 1957:38
*Colladonus belli:* Metcalf 1967:1245
*Thamnotettix semipullatus* Van Duzee 1892:306
*Colladonus semipullatus:* Oman 1949:125
*Thamnotettix gilletti* Van Duzee 1892:306
*Colladonus gilletti:* Oman 1949:125
*Thamnotettix sonorae* Gillette & Baker 1895:100
*Colladonus sonorae:* Oman 1949:125

LENGTH.—Male, 4.0–4.4 mm; female, 4.4–5.2 mm.

A well-marked species from pale yellow to deep yellow with two black spots on anterior margin of crown and sometimes with a black, transverse band on disc of crown; pronotum with pale yellow to deep yellow, transverse band; forewings with veins pale to yellow; color intensity highly variable. Similar to *fasciaticollis* in general habitus but with distinctive male genitalia.

Head with anterior margin not produced, apex rounded.

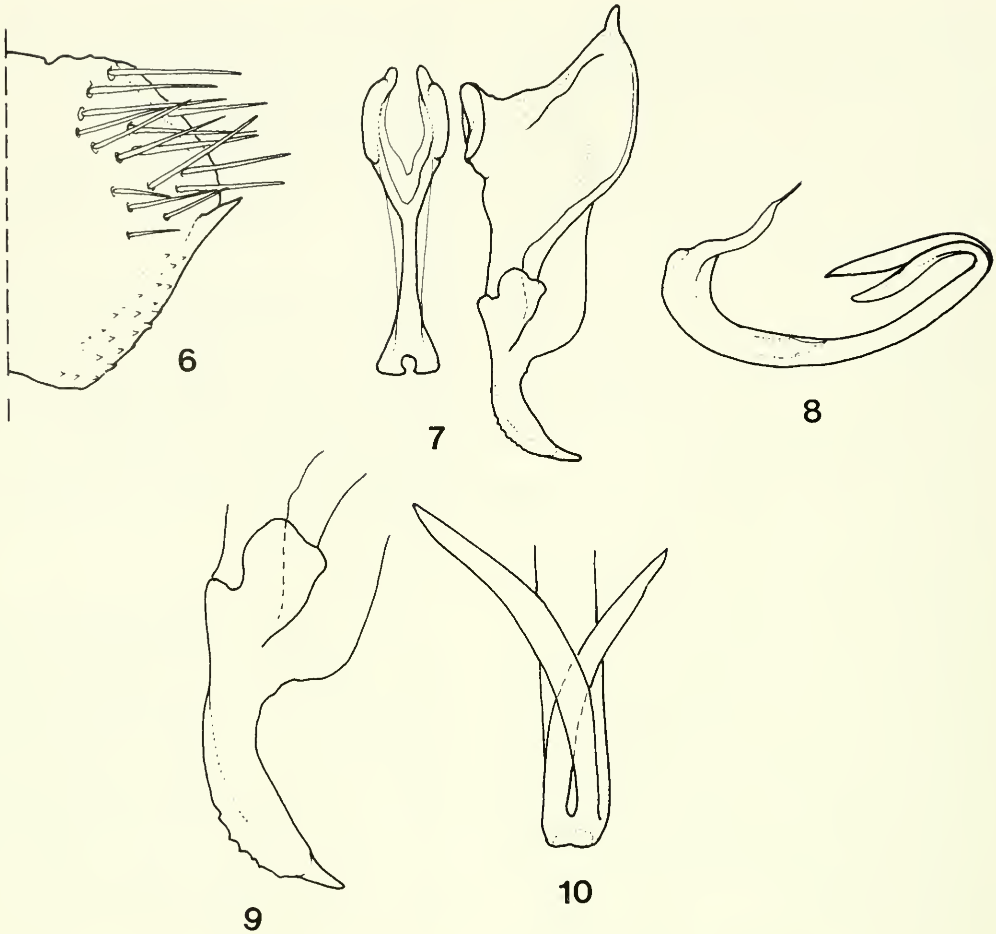
MALE.—Pygofer in lateral view with short, stout spine near or above middle of caudal margin, spine projecting dorsally (Fig. 6); aedeagus in lateral view with long, bifurcated distal processes extending beyond midlength of shaft (Fig. 8), crossing over in dorsal view (Fig. 10), gonopore about middle of shaft; connective short, not reaching apex of style (Fig. 7); style with moderately broad stylar shaft, inner lateral margin serrate, outer one smooth, stylar spine moderately long, projecting laterally (Fig. 9).

FEMALE.—Seventh sternum with truncate caudal margin, shallow, U-shaped excision medially.

DISTRIBUTION.—This species is widespread in mountainous areas from Mexico north to British Columbia. In Mexico the author collected specimens in the state of Chihuahua. It has been reported in seven western states in the United States and in the province of British Columbia (Nielson 1957).

HOST.—Adults have been swept from a variety of trees and shrubs by the author. Several specimens were taken from *Monarda* sp. near *citriodora* Cerv. in Chihuahua state in Mexico by the author.

REMARKS.—*Colladonus belli* may represent a species complex that occupies a rather narrow, longitudinal range in western North America. Specimens north of Utah and Colorado are almost uniformly yellow-green without a dark band across the crown, whereas southern populations are more



Figs. 6-10. *Colladonus belli* (Uhler): 6, male pygofer, lateral view; 7, connective and right style, dorsal view; 8, aedeagus, lateral view; 9, apex of right style, enlarged dorsal view; 10, apex of aedeagus and distal processes, dorsal view.

deeply marked with yellow and black markings. The position of the pygofer spine, although similar in configuration, varies from distad of the middle of the caudal margin in northern populations to the middle of the caudal margin in southern populations. No variation in the configuration of the female seventh sternum was evident, however.

Much additional collecting over the entire range of this species complex is needed. Populations are not commonly collected, and when found, specimens are usually few in number. A reexamination of the type specimens of *belli*, *semipullatus*, *gillettei*, and *sonorae* is recommended for any future study.

From *fasciaticollis*, to which it is similar, *belli* can be distinguished by the short pygofer species has been made, nor has any type of dle to upper middle portion of the caudal margin.

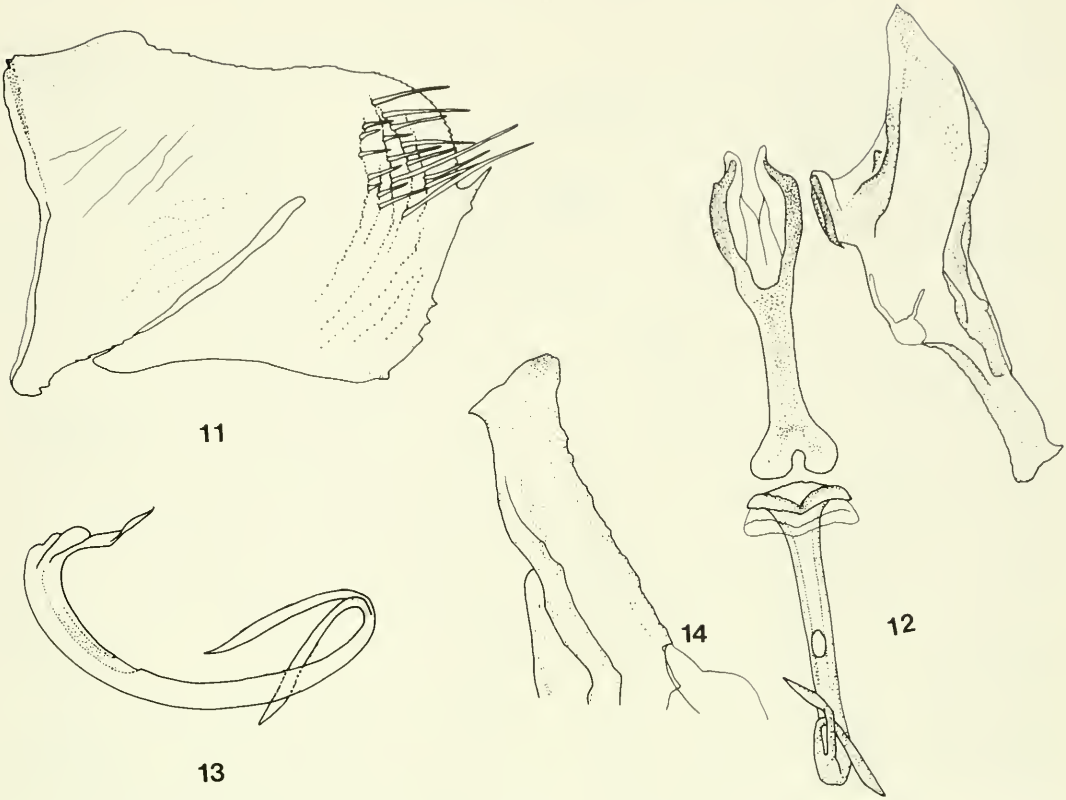
*Colladonus serratus*, n. sp.
Figs. 11–14

LENGTH.—Male, 4.8–5.0 mm; female, 5.4 mm.

Color dark brown to blackish; crown yellow with two large, quadrate, black spots on anterior margin, disc with broad, black, transverse band; pronotum with yellow, narrow to broad, transverse band; forewings black except for translucent area along middle of costa, veins yellow; face yellow with black markings.

Head with anterior margin produced, apex obtusely angled.

MALE.—Pygofer in lateral view with broadly rounded caudal margin, caudoventral




Figs. 11-14. *Colladonus serratus*, n. sp.: 11, male pygofer, lateral view; 12, connective, right style, and aedeagus, dorsal view; 13, aedeagus, lateral view; 14, apex of right style, enlarged dorsal view.

margin toothed or serrate, short spine above middle of caudal margin, directed dorsad (Fig. 11); aedeagus in lateral view narrow along major portion of shaft with moderately long, distal, bifurcated processes reaching to about middle of shaft (Fig. 13), processes broad medially, gradually tapered distally, crossing over in dorsal view (Fig. 12), gonopore basad of middle of shaft; connective short, not reaching apex of style (Fig. 12); style with broad stylar shaft, stylar spine subapical, small, sharply pointed (Fig. 14).

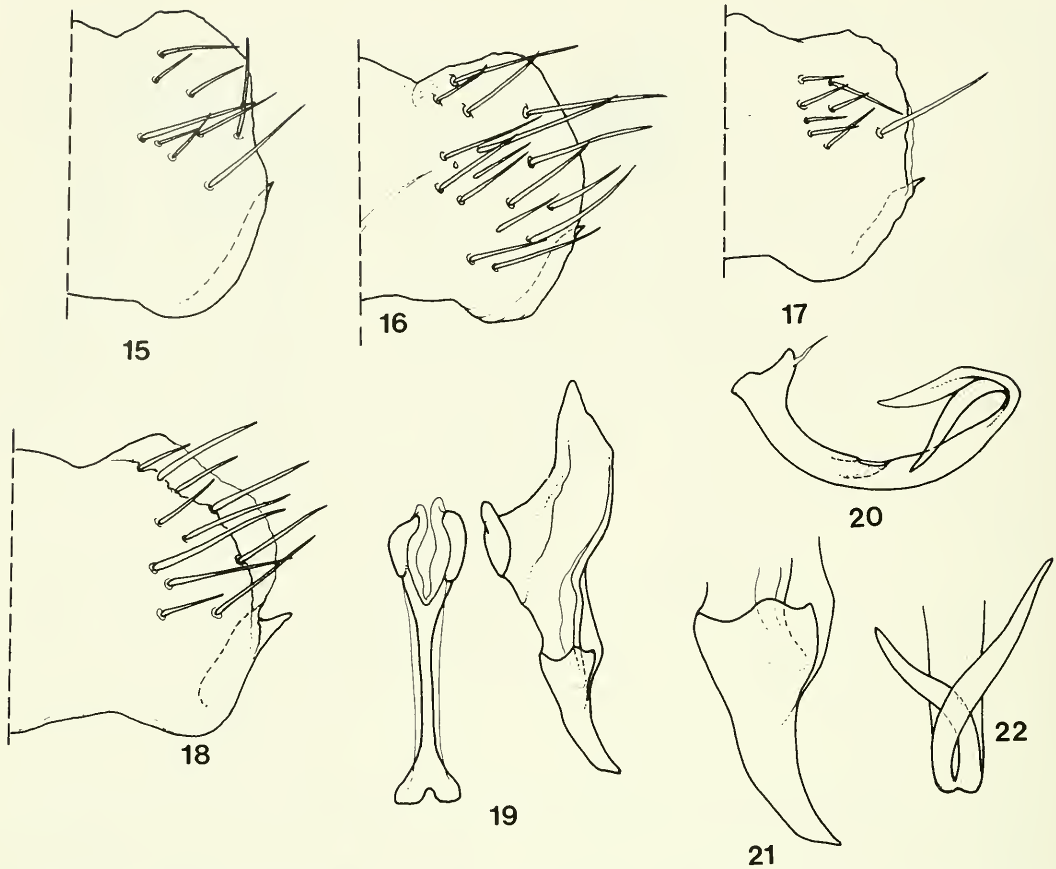
FEMALE.—Seventh sternum with truncate caudal margin, small tooth medially.

HOLOTYPE (male).—MEXICO: Mex., 7 miles east of Amecameca, 9,300 ft, 31.VI.1974, C. W. and L. O'Brien and Marshal (USNM). Allotype female, same locality as holotype, 10,000 ft, 17.VIII.1982, C. W. and L. O'Brien and G. Wibner (USNM). Paratypes: one male, same data as female allotype (in author's collection); one male, Mexico, #16, 7 miles southeast of Amecameca, 9,000 ft, 17.VIII.1969, George W. Byers (UK).

REMARKS.—This is a rather unique species that is not related to other species of *Colladonus* in Mexico. The combination of the subapical stylar spine and toothed caudoventral margin of the pygofer will readily distinguish it from all other known species in the region.

### *Colladonus fasciaticollis* (Stal)
Figs. 15–22

*Jassus fasciaticollis* Stal 1864:86 [Holotype ♀ (NM) (examined).]
*Thamnotettix fasciaticollis:* DeLong 1946:13
*Colladonus fasciaticollis:* Nielson 1957:37
*Thamnotettix fasciaticollis:* Metcalf 1967:756
*Idiodonus tubulus* DeLong 1946:22 [Holotype ♀ (OSU) (examined).]
*Colladonus tubulus:* Nielson 1957:37
*Idiodonus tubulus:* Metcalf 1967:1303
*Idiodonus tubulus:* DeLong 1984:10
*Idiodonus diserus* DeLong 1946:24 [Holotype ♀ (OSU) (examined).]
*Colladonus diserus:* Nielson 1957:37
*Idiodonus diserus:* Metcalf 1967:1297
*Idiodonus diserus:* DeLong 1984:11
*Idiodonus pravus* DeLong 1946:24 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus pravus:* Metcalf 1967:1301
*Idiodonus pravus:* DeLong 1984:11
*Idiodonus dampfi* DeLong 1946:20 [In part, allotype ♂ and 8 paratypes (OSU)]
*Idiodonus dampfi:* Linnavuori 1959:280 [Misdetermined specimens.]




Figs. 15–22. *Colladonus fasciaticollis* (Stal): 15, male pygofer of specimen from Costa Rica, lateral view; 16, male pygofer of allotype of *tubulus*, lateral view; 17, male pygofer of allotype of *diserus*, lateral view; 18, male pygofer of allotype of *dampfi* (=*fasciaticollis*), lateral view; 19, connective and right style, dorsal view; 20, aedeagus, lateral view; 21, apex of right style, enlarged dorsal view; 22, apex of aedeagus and distal processes, enlarged dorsal view.

LENGTH.—Male, 4.4–4.6 mm; female, 4.8–5.0 mm.

A well-marked black and yellow species usually, but sometimes paler in some specimens. Similar in general habitus to *belli* and to *albocinctus* in male genitalic characters but distinct from both species.

Head with anterior margin not produced, apex nearly rounded.

MALE.—Pygofer in lateral view with short, bluntly pointed spine arising below middle of caudal margin (some variation in origin of spine on caudoventral margin), basal 3/4 of spine sclerotized and fused to pygofer wall (Figs. 15, 16, 17, 18); aedeagus in lateral view with moderately long and narrow (sometimes broad), distal, bifurcated processes extending to about middle of shaft (Fig. 20), crossing over in dorsal view (Fig. 22), gonopore at about middle of shaft; connective short, apex not reaching to apex of style (Fig. 19); style with tapered stylar shaft, lateral margins smooth, stylar spine slanted laterodistally (Fig. 22).

FEMALE.—Seventh sternum with caudal margin obtusely angled with shallow, U-shaped, median emargination.

DISTRIBUTION.—*Colladonus fasciaticollis* is widely distributed from southern California to Costa Rica. Its northern range into the United States is restricted to the southern border of California. It is common in southern Mexico in the states of Distrito Federal, Veracruz, Michoacán, and Puebla.

HOST.—This species presumably occurs on unspecified trees or shrubs in Mexico from September to November at elevations from

5,000 to 10,000 feet (DeLong 1946). In Costa Rica it was taken on *Lippia berlandieri* in February (Nielson 1957).

REMARKS.—In my earlier work (Nielson 1957), *tubulus* and *diserus* were transferred to *Colladonus* and suppressed as synonyms of *fasciaticollis*. Reexamination of the female holotypes and comparison of them with authentically determined female specimens of *fasciaticollis* confirm that action.

The female holotype of *pravus* is identical to its counterpart holotype specimens of the above species. The male allotype of *dampfi* from Bella Vista, Mexico (MB 366), which apparently had been misidentified and improperly associated with the female holotype, was associated with the male holotype of *pravus* from Zitacuaro, Michoacán. Two of five male paratype specimens and three female paratype specimens of *dampfi* from Orizaba, Veracruz, were also associated with *pravus*.

From *albocinctus* and *belli*, to which it has similar genitalia, *fasciaticollis* can be distinguished by the pygofer spine that arises from near the middle of the caudal margin, the shorter aedeagus, and the stouter, bifurcated distal processes.

### *Colladonus ultimus*, n. sp.
Figs. 23–26

LENGTH.—Male, 3.9–4.2 mm; female, 4.7–4.9 mm.

General color dark brown to black; crown yellow with two black spots on anterior margin and narrow, black, transverse band between eyes; pronotum black with narrow, yellow, transverse band at middle; forewings black with yellow veins, costal area hyaline; face yellow with black markings. Similar in general habitus to *dampfi* (DeLong) but with distinctive male genitalia.

Head with anterior margin produced, apex rounded.

MALE.—Pygofer in lateral view with caudal margin broadly rounded, pygofer spine short, slightly longer than basal width, arising just below midline of pygofer and projecting caudodorsally (Fig. 23); aedeagus in lateral view with narrow shaft, distal, bifurcated processes long, more than 1/2 length of shaft and extending beyond gonopore (Fig. 25), processes of uniform width except for tapered apex, gonopore at about midlength of shaft; connective short, apex not reaching apex of style (Fig. 24); style with broad stylar shaft, nearly straight, stylar spine short, sharply pointed distally and projecting laterally (Fig. 26).

FEMALE.—Seventh sternum with caudal margin nearly truncate, with small indentation medially.

HOLOTYPE (male).—PANAMA: Chiriqui, Bambito, 1,400 m, 10.VI.1976, Wolda and Estribi (USNM).

REMARKS.—Numerous specimens of this species that were collected in Costa Rica and preserved in alcohol were too badly distorted and discolored to be used in the type series. They were all taken at Cerro de la Muerte, 10,000 ft, 1.VIII.1966, S. L. Wood, and are in the M. L. Bean Museum collection. A single female specimen of this species from Yepocapa, Guatemala, XII.1948, H. T. Dalmat, was also examined.

This species thus far represents the southernmost extremity of the range of *Colladonus*. It can be distinguished from *dampfi* by the shorter pygofer spine, by the gonopore, which lies midlength of the aedeagal shaft, and by the shorter connective.

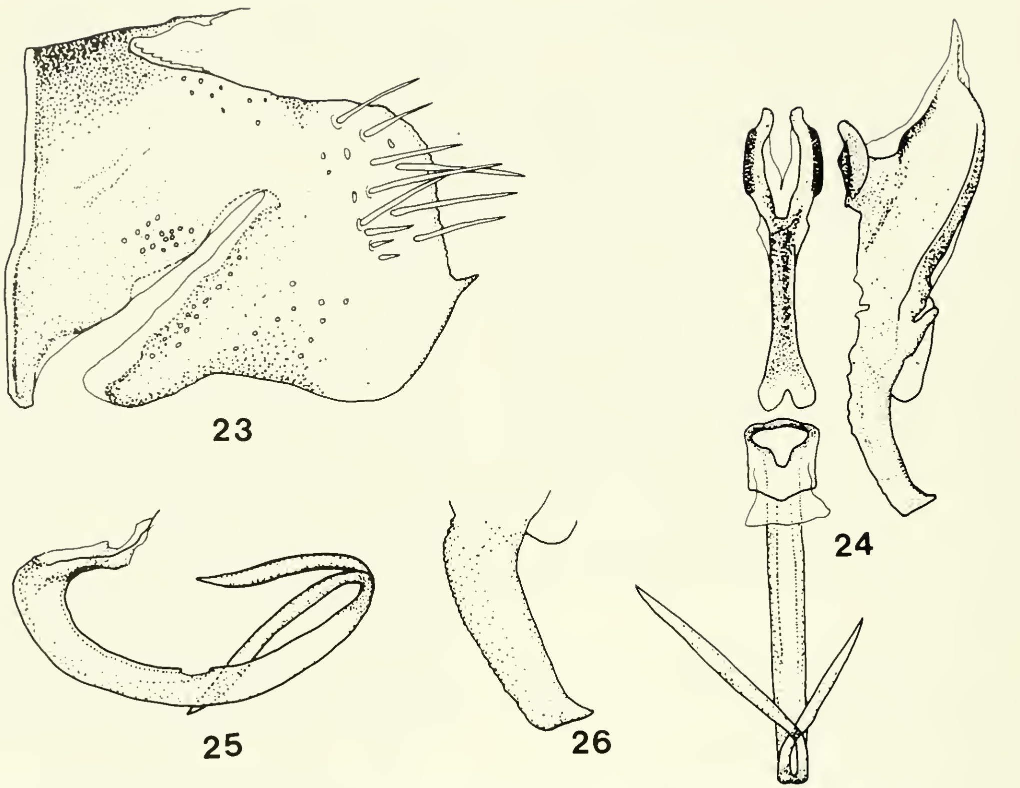
### *Colladonus tolucensis*, n. sp.
Figs. 27–30

LENGTH.—Male, 4.5–4.6 mm; female, 5.0–5.2 mm.

Color tan with black markings; crown with two spots on anterior margin, black, transverse band on middle of crown; pronotum with broad, pale ivory, transverse band, sometimes with broken black stripe on either side of middle; forewings with pale veins, clavus sometimes dark brown, and with dark brown, longitudinal stripe above costal cell; face deep tan with black markings on clypeus. Similar in general habitus to several species possessing broad pronotal band and in male genital characters to *ultimus*.

Head with anterior margin produced, apex obtusely angled.

MALE.—Pygofer in lateral view with broad, obtusely rounded caudal margin, very short spine arising from middle of margin and sometimes hidden from lateral view, projecting distally (Fig. 27); aedeagus in lateral view with narrow shaft, distal, bifurcated processes long, extending slightly beyond midlength of shaft (Fig. 29), processes broad medially, pointed distally, gonopore at about midlength




Figs. 23–26. *Colladonus ultimus*, n. sp.: 23, male pygofer, lateral view; 24, connective, right style, and aedeagus, dorsal view; 25, aedeagus, lateral view; 26, apex of right style, enlarged dorsal view.

of shaft; connective short, not reaching apex of style (Fig. 28); style with tapered stylar shaft, stylar spine small, directed laterodistally (Fig. 30).

FEMALE.—Seventh sternum with caudal margin nearly truncate, with broad median excavation.

HOLOTYPE (male).—MEXICO: Distrito Federal, Toluca road, 26.IX.1945, DeLong, Hershberger, and Elliot (OSU), allotype female, Mexico City, D.F., 13.IX.1939, D. M. DeLong (OSU). Paratypes: one male, same data as holotype (in author's collection); one female, same data as allotype (in author's collection); 29 females, same data as allotype (OSU).

REMARKS.—From *ultimus*, to which it is similar, *tolucensis* can be distinguished by the unexposed pygofer spine, by the tapered stylar shaft, and by the color patterns on the pronotum.

## *Colladonus dampfi* (DeLong)

Figs. 31–34

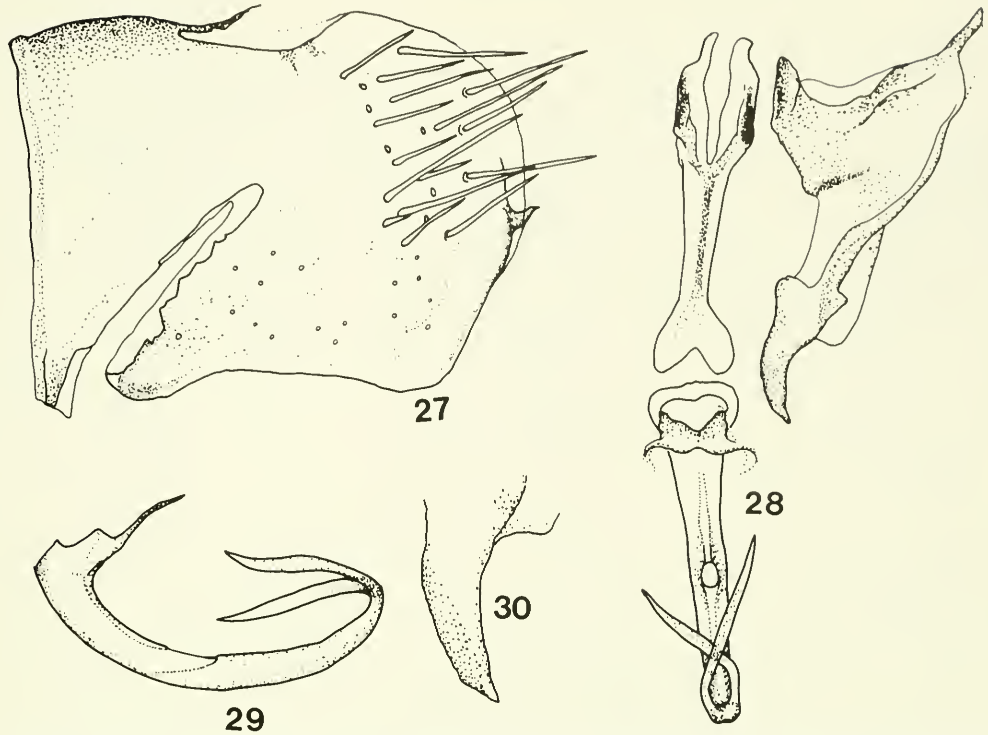
*Idiodonus dampfi* DeLong 1946:20 [Holotype ♀ (OSU) (examined).]
*Colladonus dampfi:* Nielson 1957:51
*Idiodonus dampfi:* Metcalf 1967:1297
*Idiodonus dampfi:* DeLong 1984:11

LENGTH.—Male, 3.9–4.0 mm; female, 4.5 mm.

A well-marked, black and yellow species with two distinct, black spots on anterior margin of crown, narrow, transverse, black band on disc; pronotum with broad, black band along anterior margin, broad, yellow, transverse band medially, narrow, black band on posterior margin; forewings with pale yellow to deep yellow veins, cells brown to black. Similar to other pronotal banded species and to *bicinctus* (DeLong) in male genital characters.

Head with anterior margin not produced, apex obtusely rounded.

MALE.—Pygofer in lateral view with moderately long, narrow spine arising from middle of caudal margin and projecting dorsally




Figs. 27–30. *Colladonus tolucensis*, n. sp.: 27, male pygofer, lateral view; 28, connective, right style, and aedeagus, dorsal view; 29, aedeagus, lateral view; 30, apex of right style, enlarged dorsal view.

(Fig. 31); aedeagus with distal, bifurcated processes long, extending beyond midlength of shaft (Fig. 33), crossing over in dorsal view, gonopore basad of middle of shaft; connective long, extending to about apex of style (Fig. 32); style with narrow stylar shaft, inner lateral margin roughly dentate, stylar spine long and projecting laterally (Fig. 34).

FEMALE.—Seventh sternum with caudal margin narrowed distally, shallow, U-shaped indentation medially.

DISTRIBUTION.—*Colladonus dampfi* is known only from the Mexican states of Veracruz and Morelos.

HOST.—Recorded from unspecified trees and shrubs from 3,000 to 9,000 feet during September to November (DeLong 1946).

REMARKS.—The type series of *dampfi* is mixed. The female holotype and male allotype were not properly associated; the latter is identical to *pravus*, which is treated as a junior synonym of *fasciaticollis* in this paper. A male paratype of *dampfi* from Cordoba, Veracruz (type locality), was associated with the female holotype of *dampfi* and used in illustrating the male genitalia. Five additional male paratypes, three from Cuernavaca, Morelos, and two from unspecified localities (MB 95, Mexico, and MF 8523, Mexico) were identical to the male paratype specimen associated with the female holotype. The remaining specimens in the type series are discussed under *fasciaticollis*.

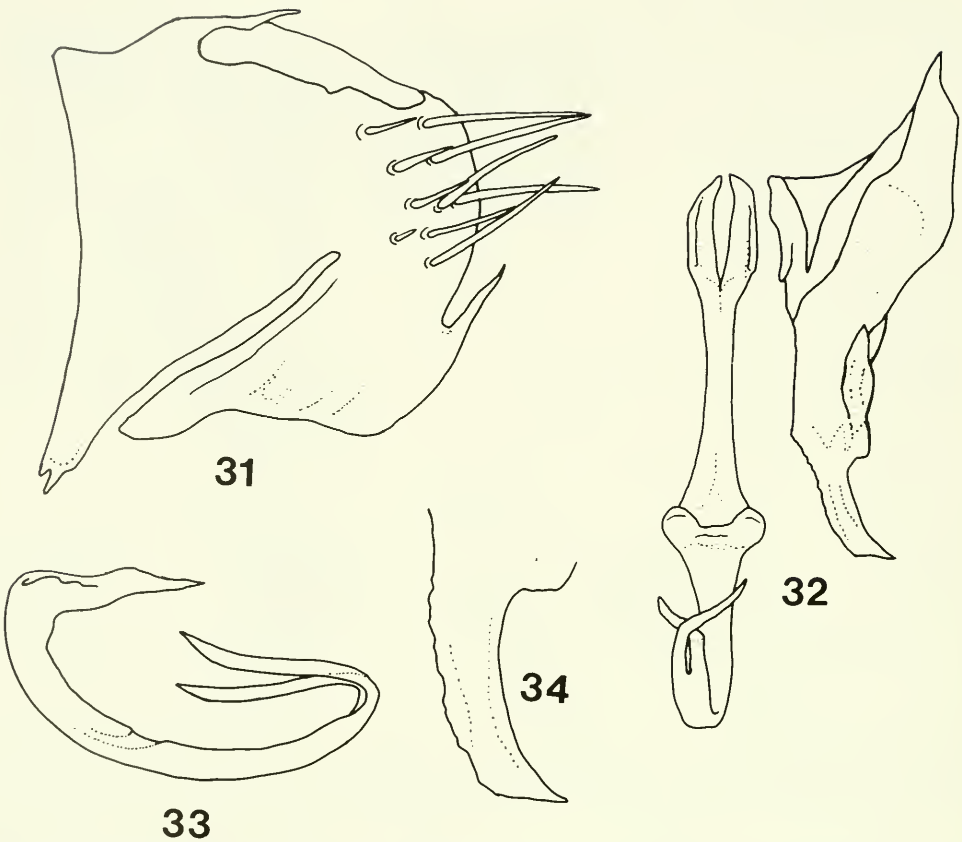
*Colladonus dampfi* can be distinguished from *bicinctus* by the short and more rounded anterior margin of the head, by the longer pygofer spine, and by the longer, distal, bifurcated aedeagal processes.

## *Colladonus bicinctus* (DeLong)
Figs. 35–39

*Idiodonus bicinctus* DeLong 1946:18 [Holotype ♀ (OSU) (examined).]
*Colladonus bicinctus:* Nielson 1957:51
*Idiodonus bicinctus:* Metcalf 1967:1287
*Idiodonus bicinctus:* DeLong 1984:10

LENGTH.—Male, 4.2 mm; female, 4.5–4.8 mm.

A well-marked species of deep yellow with black markings; crown with two triangular,




Figs. 31–34. *Colladonus dampfi* (DeLong): 31, male pygofer, lateral view; 32, connective, right style, and aedeagus, dorsal view; 33, aedeagus, lateral view; 34, apex of right style, enlarged dorsal view.

black spots on anterior margin and narrow, black, transverse band on middle of disc; pronotum with narrow, black band along anterior margin and narrow, black, transverse band on middle transecting broad, yellow, transverse band; forewings with veins yellow, cells black. Similar in general habitus and male genitalic characters to *claustrus* (DeLong).

Head with anterior margin produced, apex angled.

MALE.—Pygofer in lateral view with moderately long spine on middle of caudal margin, spine directed caudodorsally (Fig. 35); aedeagus in lateral view with stout, distal, bifurcated processes reaching to about midlength of shaft (Fig. 37), not crossing over in dorsal view (Fig. 39), gonopore slightly basad of midlength of shaft; connective short, not reaching apex of style (Fig. 36); style with narrow stylar shaft, lateral margins smooth, stylar spine very short and bluntly pointed (Fig. 38).

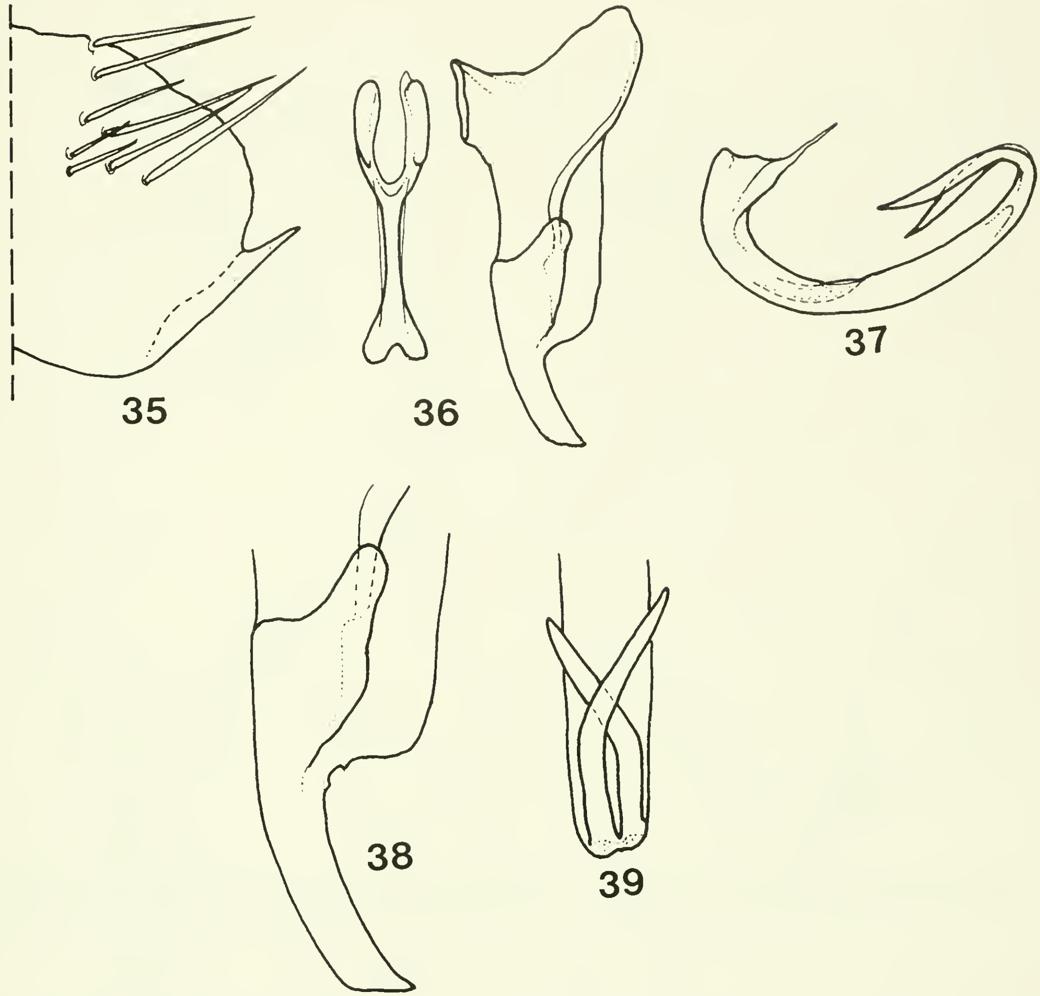
FEMALE.—Seventh sternum with caudal margin shallowly and broadly concave, small indentation medially.

DISTRIBUTION.—This species is known only from the Mexican state of Distrito Federal.

HOST.—According to DeLong (1946) the species was collected at 7,500 feet from unspecified shrubs or trees during a June–September period.

REMARKS.—This species was described from the female holotype and a female paratype specimen. However, a male paratype specimen (MB 352, Mexico, A. Dampf, coll.), which was without a name label and not cited in the original description, was found among the type series. The specimen was associated with the female holotype and used in illustrating the genitalia.

The species can be separated from *claustrus* by the presence of a narrow, transverse, black band on the middle of the pronotum, by the narrower pygofer spine, by the shorter




Figs. 35–39. *Colladonus bicinctus* (DeLong): 35, male pygofer, lateral view; 36, connective and right style, dorsal view; 37, aedeagus, lateral view; 38, apex of right style, enlarged dorsal view; 39, apex of aedeagus and distal processes, enlarged dorsal view.

connective, and by the smooth-margined stylar shaft.

### *Colladonus claustrus* (DeLong)
Figs. 40–44

*Idiodonus claustrus* DeLong 1946:18 [Holotype ♀ (OSU) (examined).]
*Colladonus claustrus:* Nielson 1957:51
*Idiodonus claustrus:* Metcalf 1967:1289
*Idiodonus claustrus:* DeLong 1984:11

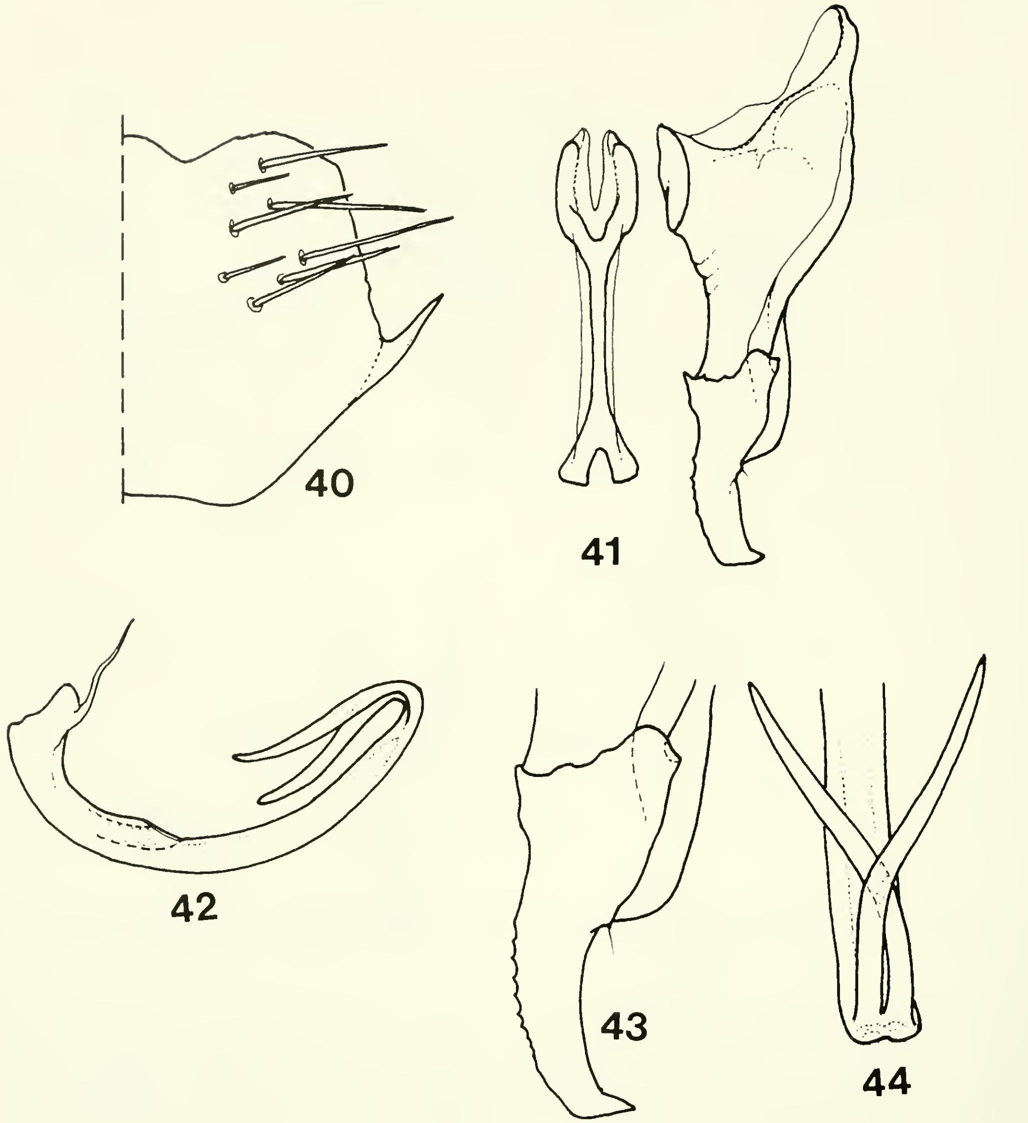
LENGTH.—Male, 4.4 mm; female, 4.8–5.0 mm.

A well-marked species with color patterns nearly identical to *bicinctus* except paler and without median, transverse, black band on pronotum. Similar in male genital characters to *bicinctus*.

Head with anterior margin produced, apex angled.

MALE.—Pygofer in lateral aspect with moderately long, stout spine on middle of caudal margin, spine directed caudodorsally (Fig. 40): aedeagus with slender, bifurcated, distal processes reaching to about middle of shaft, apices not reaching gonopore (Fig. 42), crossing over in dorsal view (Fig. 44), gonopore basad of midlength of shaft; connective short, not reaching apex of style (Fig. 41); style with inner lateral margin serrate, outer one smooth, stylar spine short, bluntly pointed and directed laterad (Fig. 43).

FEMALE.—Seventh sternum with caudal margin shallowly and broadly concave, small




Figs. 40–44. *Colladonus claustrus* (DeLong): 40, male pygofer, lateral view; 41, connective and right style, dorsal view; 42, aedeagus, lateral view; 43, apex of right style, enlarged dorsal view; 44, apex of aedeagus and distal processes, enlarged dorsal view.

indentation medially.

DISTRIBUTION.—This species is known only from the Mexican states of Veracruz and Chiapas.

HOST.—Specimens were collected on unspecified shrubs or trees at elevations between 4,000 and 7,000 feet from August to October (DeLong 1946).

REMARKS.—The female holotype and male allotype, although from widely separate localities, appear to be properly associated. From *bicinctus*, to which it is closely related, *claustrus* can be separated by the absence of the narrow, transverse, black band on the middle of the pronotum, by the stouter pygofer spine, by the serrated, inner lateral margin of the stylar shaft, and by the more basad position of the gonopore.

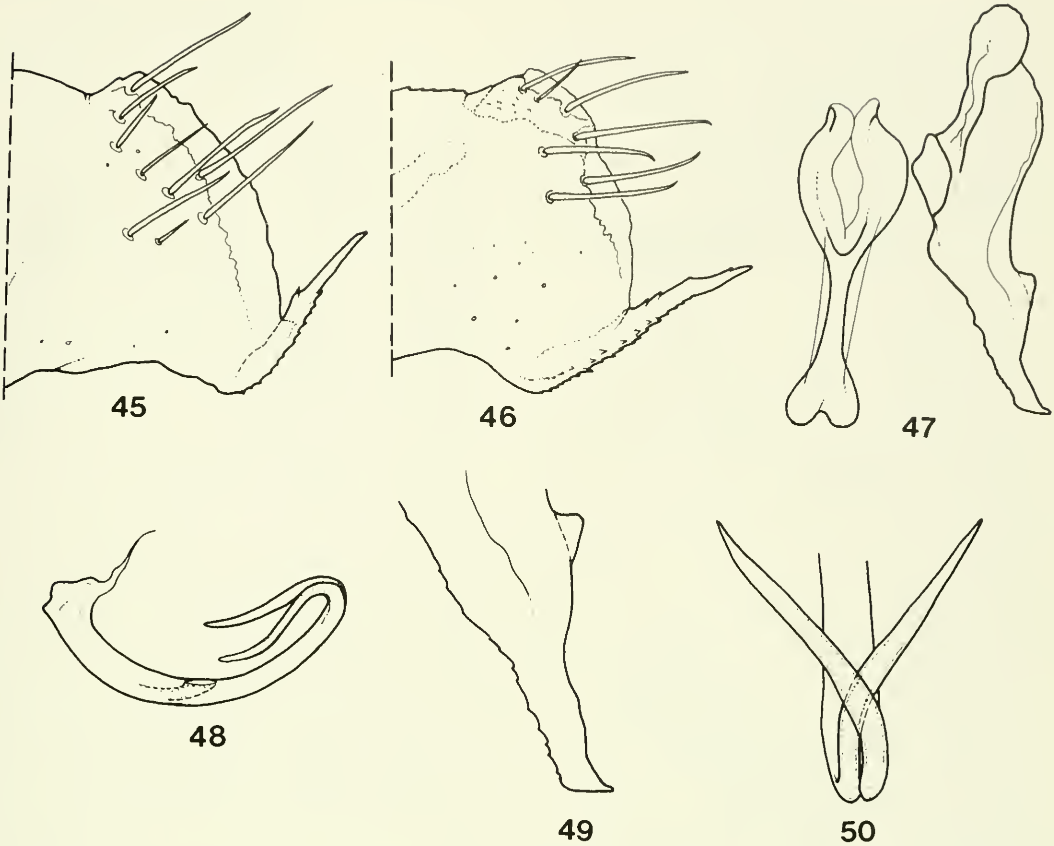
### *Colladonus verecundus* (DeLong)

Figs. 45–50

*Idiodonus verecundus* DeLong 1946:20 [Holotype ♀ (OSU) (examined).]

*Colladonus verecundus:* Nielson 1957:51

*Idiodonus verecundus:* Metcalf 1967:1304




Figs. 45–50. *Colladonus verecundus* (DeLong): 45, male pygofer (allotype of *verecundus*), lateral view; 46, male pygofer (allotype of *acus*), lateral view; 47, connective and right style, dorsal view; 48, aedeagus, lateral view; 49, apex of right style, enlarged dorsal view; 50, apex of aedeagus and distal processes, enlarged dorsal view.

*Idiodonus verecundus:* DeLong 1984:11
*Idiodonus acus* DeLong 1946:20 [Holotype ♀ (OSU) (examined).] New synonymy
*Colladonus acus:* Nielson 1957:51
*Idiodonus acus:* Metcalf 1967:1286
*Idiodonus acus:* DeLong 1984:11
*Idiodonus mexicanus:* DeLong 1946:27 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus mexicanus:* Metcalf 1967:1300
*Idiodonus mexicanus:* DeLong 1984:11

LENGTH.—Male, 4.5–4.6 mm; female, 4.9–5.0 mm.

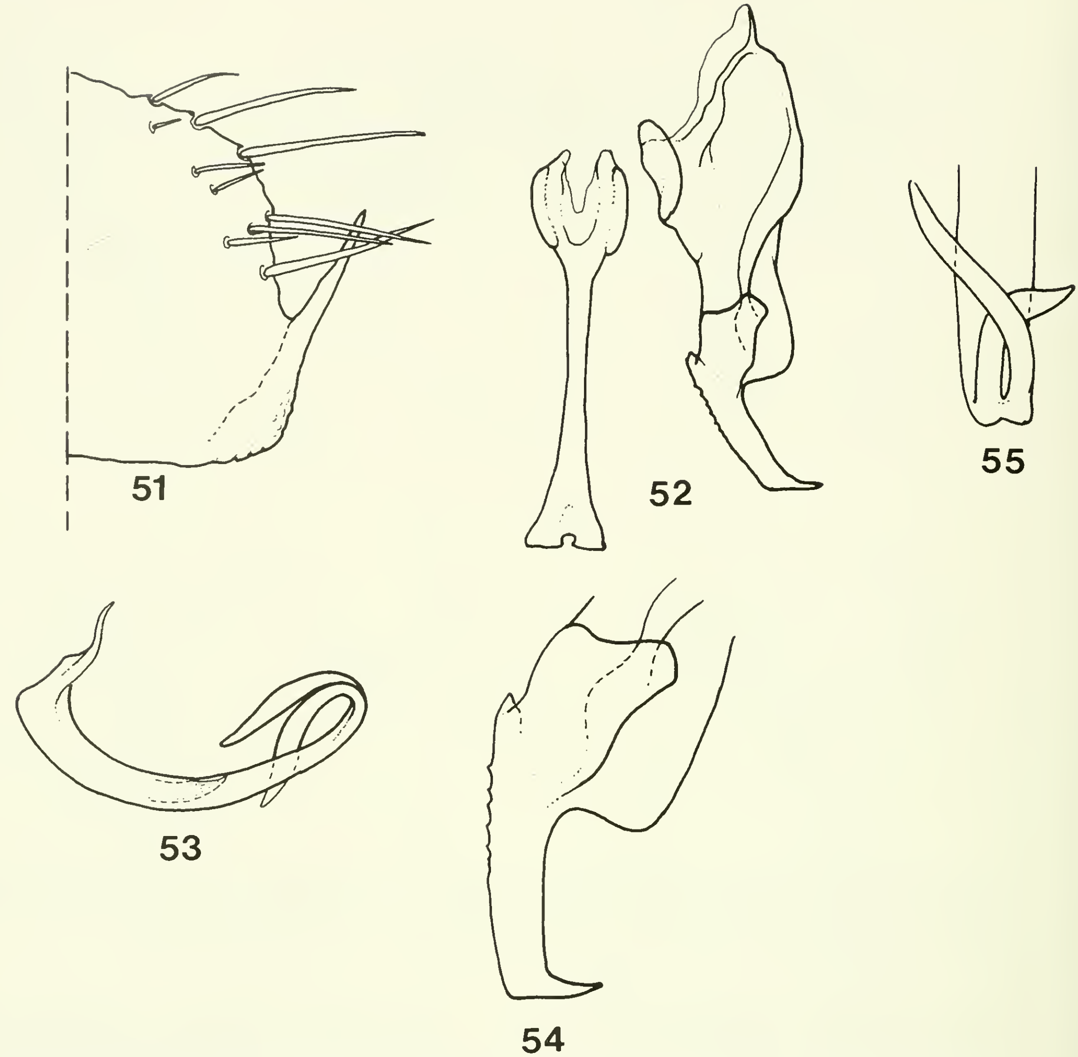
A well-marked species with two distinctive, black spots on anterior margin of crown and narrow to broad, ivory or yellow, transverse band along middle of pronotum. Similar to other pronotal banded species, but with unique pygofer spine.

Head with anterior margin produced, apex angled.

MALE.—Pygofer in lateral view with long, dentate caudoventral spine, spine projecting caudodorsally with its exposed distal part about 1/2 as long as its entire length from its basal origin (Figs. 45, 46); aedeagus in lateral view with bifurcated distal processes about 1/2 as long as shaft, apices reaching gonopore (Fig. 48), crossing over in dorsal view (Fig. 50), gonopore at midlength of shaft; connective long, extending distally beyond apex of style (Fig. 47); style with stylar shaft serrate on inner lateral margin with short stylar spine projecting laterally (Fig. 49).

FEMALE.—Seventh sternum with caudal margin slightly rounded or angled on either side of median, shallow indentation; sometimes with slight protrusion laterally next to indentation.

DISTRIBUTION.—This species is restricted to the Mexican states of Distrito Federal, Michoacán, and Morelos.




Figs. 51–55. *Colladonus titulus* (DeLong): 51, male pygofer, lateral view; 52, connective and right style, dorsal view; 53, aedeagus, lateral view; 54, apex of right style, enlarged dorsal view; 55, apex of aedeagus and distal processes, enlarged dorsal view.

HOST.—Specimens were collected on pine at elevations from 9,500 to 10,300 feet during September and October (DeLong 1946).

REMARKS.—The female seventh sterna of the holotypes of *verecundus* and *mexicanus* are identical in configuration. In *acus* the lateral margins are angled toward the middle. I consider these traits normal variation in the population. The sexes of each species of *verecundus* and *acus* appear to be properly associated, although there is some variation in color between the two species. The color patterns and configuration of the seventh sternum of the holotype of *mexicanus* are similar to *verecundus*. The male genitalic features of the allotypes of *acus* and *verecundus* are identical.

This species can be distinguished from all members of the genus *Colladonus* by its unique, very long, dentate pygofer spine.

*Colladonus titulus* (DeLong)
Figs. 51–55

*Idiodonus titulus* DeLong 1946:24 [Holotype ♂ (OSU) (examined).]
*Colladonus titulus:* Nielson 1957:51
*Idiodonus titulus:* Metcalf 1967:1302
*Idiodonus titulus:* DeLong 1984:11
*Idiodonus goodi:* DeLong 1946:27 [Holotype ♀ (OSU)

(examined).] New synonymy
*Idiodonus goodi:* Metcalf 1967:1298
*Idiodonus goodi:* DeLong 1984:11

LENGTH.—Male, 4.4–4.6 mm; female, 4.9–5.2 mm.

General color light tannish to yellow with deep fuscous to black markings on crown, pronotum, and forewings; crown with two subtriangular spots on anterior margin; pronotum with anterior border black, broad, transverse, tannish band below; forewings with veins tannish to yellow, cells suffused with light fuscous to black. Similar in general habitus and certain male genital characters to *claustrus*, but more nearly related in male genital characters to *singularius*.

Head with anterior margin not produced, apex slightly angled.

MALE.—Pygofer in lateral view with long spine arising about middle of caudal margin and directed nearly dorsad (Fig. 51); aedeagus in lateral view with short, rather stout, distal, bifurcated processes not reaching midlength of shaft (Fig. 53), crossing over in dorsal view (Fig. 55), gonopore slightly distad of middle of shaft; connective long, extending distad of apex of style (Fig. 52); style with narrow stylar shaft, stylar spine long, narrow, directed laterad (Fig. 54).

FEMALE.—Seventh sternum with caudal margin slightly produced along middle, with small excision at middle.

DISTRIBUTION.—This species is known only from the Mexican states of Distrito Federal and Veracruz.

HOST.—Reported from unspecified trees or shrubs above 7,500 feet during September and October by DeLong (1946).

REMARKS.—The male holotype and female allotype of *titulus* appear to be correctly associated. The general habitus and female seventh sternum of the holotype of *goodi* are identical to the female allotype of *titulus*. Males of *goodi* are unknown.

*Colladonus titulus* can be separated from *claustrus* by the much longer pygofer spine and from *singularius* by the shorter aedeagal processes, the more distal position of the gonopore, and the shorter stylar spine.

## *Colladonus singularius*, n. sp.

Figs. 56–59

LENGTH.—Male, 4.6 mm; female, 5.0–5.2 mm.

Color tan to pale yellow with two small spots on anterior margin of crown, narrow, dark, transverse band on middle of crown in male, marking incomplete in female; pronotum with broad, ivory, transverse band; forewings with veins pale yellow, cells translucent; face yellow with dark markings on clypeus. Similar to *belli* in general habitus but with distinctive male genitalia.

Head with anterior margin not produced, apex rounded.

MALE.—Pygofer in lateral view with produced caudoventral margin, pygofer spine very long, arising from apex of caudoventral margin and projecting caudodorsally (Fig. 56); aedeagus in lateral view with narrow shaft and long, distal, bifurcated processes extending beyond midlength of shaft (Fig. 58), crossing over in dorsal view (Fig. 57), gonopore basad of middle of shaft; connective moderately long, nearly reaching to apex of style (Fig. 57); style with narrow stylar shaft, curved laterally and with short, bluntly pointed stylar spine (Fig. 59).

FEMALE.—Seventh sternum with truncate caudal margin with small, narrow, median excision.

HOLOTYPE (male).—MEXICO: Guanajuato, 10 mi south San Luis de la Paz 24.X.1981, M. W. Nielson (Nielson collection), female allotype, same data as holotype (Nielson collection). Paratype: seven females, same data as holotype (BYU, Nielson collection).

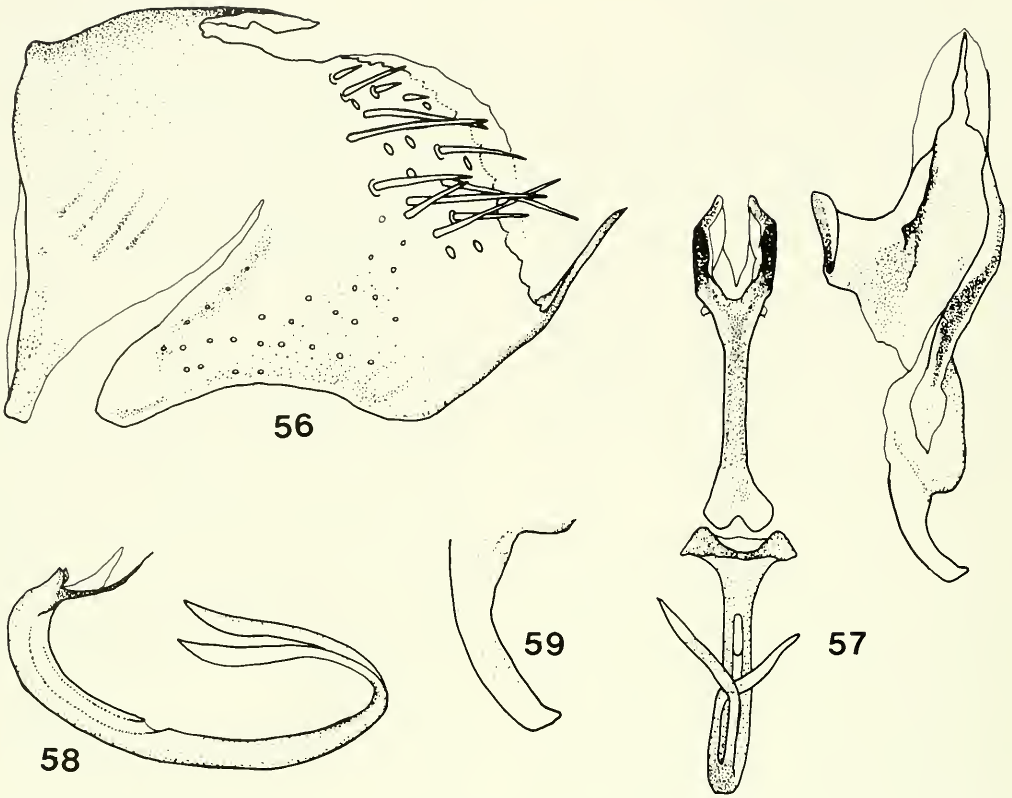
REMARKS.—From *belli*, to which it is similar in general habitus, *singularius* can be separated by the very long pygofer spine and the longer, aedeagal, bifurcated processes.

## *Colladonus trabilis*, n. sp.

Figs. 60–63

LENGTH.—Male, 4.8 mm.

COLOR.—Yellow and black. Crown yellow with two black spots on anterior margin, broad, black marking on either side of middle on disc; pronotum black with broad, yellow, longitudinal band on middle and yellow markings on lateral angles; scutellum black with large, yellow marking medially; forewings black with claval veins yellow except for black marking on basal part of posterior portion, remaining veins pale ivory, cells fuscous except in translucent costal area, first and second apical cells, and appendix; face black except yellow above. Similar to *tessellatus*.




Figs. 56–59. *Colladonus singularius*, n. sp.: 56, male pygofer, lateral view; 57, connective, right style, and aedeagus, dorsal view; 58, aedeagus, lateral view; 59, apex of right style, dorsal view.

Head with anterior margin produced, apex rounded.

MALE.—Pygofer in lateral view with acutely angled caudal margin, pygofer spine moderately long and arising from apex of caudal margin, spine curved mesad and directed caudodorsad (Fig. 60); aedeagus in lateral view with short, distal, bifurcated processes, not reaching midlength of shaft (Fig. 62), processes crossing over in dorsal view (Fig. 61), gonopore at midlength of shaft; connective long, nearly reaching to apex of style (Fig. 61); style with broad stylar shaft, curved laterad, outer lateral margin serrate, stylar spine very small, blunt distally and projecting laterally (Fig. 63).

FEMALE.—Unknown.

HOLOTYPE (male).—MEXICO: D.F., Desierto de los Leones, 9,600 ft, 6.VII.1961, George W. Byers (KU).

REMARKS.—This unusual, marked species can be distinguished from *tessellatus* by the distinctive markings on the pronotum and clavus; the broad, curved styler shaft; the shorter, distal, bifurcated processes of the aedeagus; and the gonopore at midlength of the shaft.

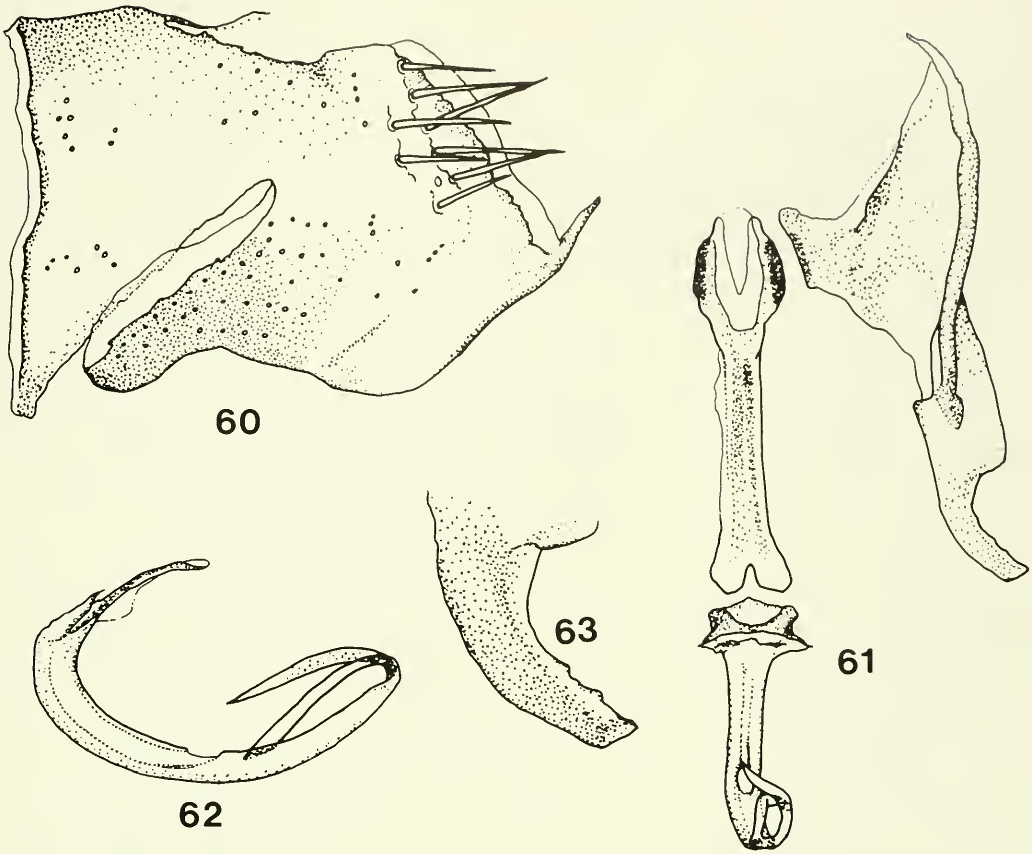
## *Colladonus clathrus* (DeLong)

Figs. 64–68

*Idiodonus clathrus* DeLong 1946:28 [Holotype ♀ (OSU) (examined).]
*Colladonus clathrus:* Nielson 1957:51
*Idiodonus clathrus:* Metcalf 1967:1288
*Idiodonus clathrus:* DeLong 1984:11
*Idiodonus turpiter* DeLong 1946:28 [Holotype ♀ (OSU) (examined).] New synonymy
*Colladonus turpiter:* Nielson 1957:51
*Idiodonus turpiter:* Metcalf 1967:1303
*Idiodonus turpiter:* DeLong 1984:10

LENGTH.—Male, 4.7–4.9 mm; female, 5.0–5.2 mm.

General color tawny with fuscous markings on disc of crown and forewings of mature specimens; crown with two distinctive, black, handlebar-shaped markings on anterior margin; pronotum without transverse band. Similar in general habitus to *anademus* (DeLong)




Figs. 60–63. *Colladonus trabilis*, n. sp.: 60, male pygofer, lateral view; 61, connective, right style, and aedeagus, dorsal view; 62, aedeagus, lateral view; 63, apex of right style, enlarged dorsal view.

but with distinctive male genitalia.

Head with anterior margin not produced, apex rounded.

MALE.—Pygofer in lateral view with long, robust spine arising from middle of caudal margin and projecting caudodorsally (Fig. 64); aedeagus in lateral view with distal, bifurcated processes more than 1/2 half as long as shaft, reflexed at distal half (Fig. 66), processes parallel in dorsal view except for distal third (Fig. 68), gonopore distad of midlength of shaft; connective long, extending beyond apex of style (Fig. 65); style with narrow stylar shaft, inner lateral margin serrate, outer one smooth, stylar spine broad, projecting laterally.

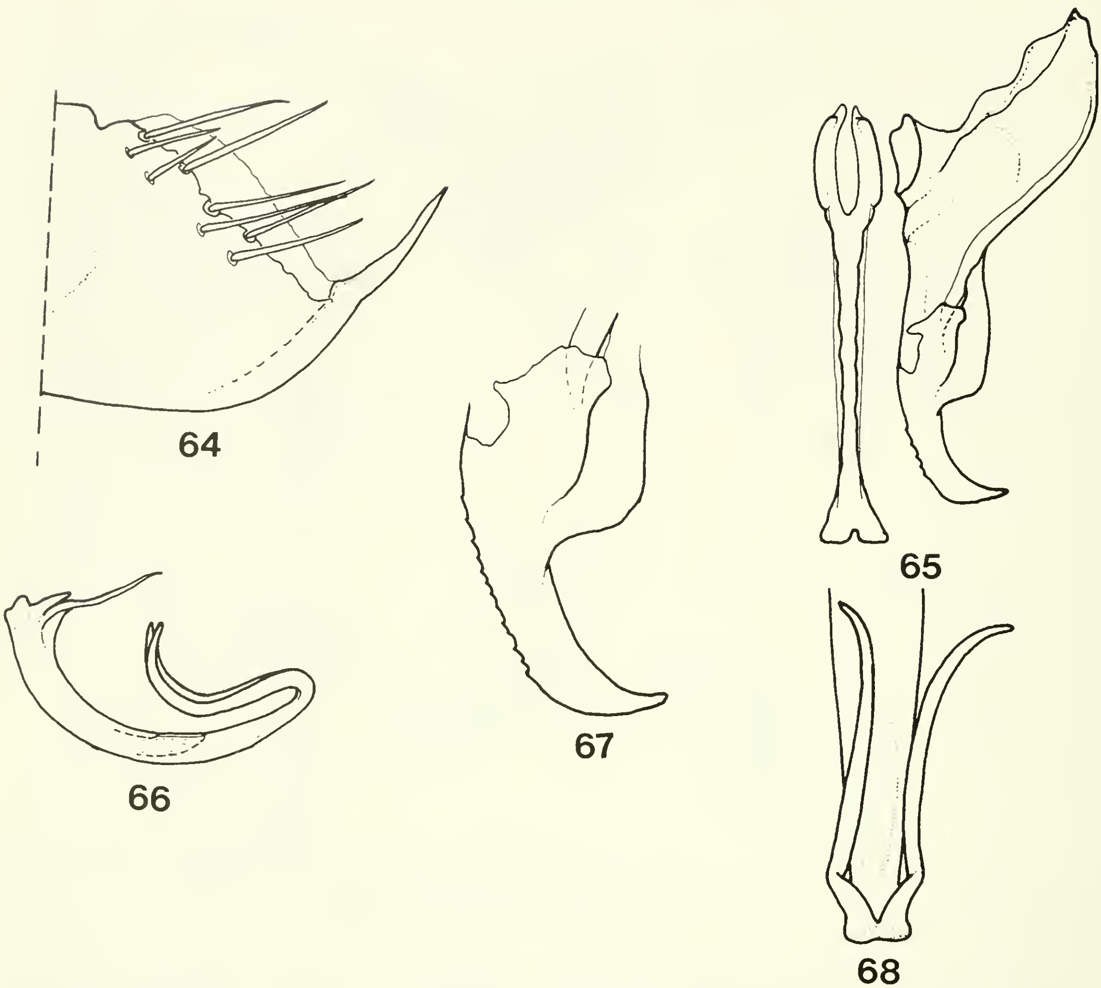
FEMALE.—Seventh sternum with broad, V-shaped, median emargination, caudal margin on either side convex.

DISTRIBUTION.—This species appears to be restricted to the Mexican state of Distrito Federal.

HOST.—Unknown.

REMARKS.—The female holotype and male allotype of *clathrus* appear to be properly associated. The female holotype of *turpiter* is identical with the female holotype of *clathrus*, based on similar color patterns (handlebar-shaped markings on anterior margin of crown) and configuration of the seventh sternum. Although DeLong did not designate an allotype of *turpiter* in his description of that species, a specimen so labeled was found and examined. This specimen could not be associated with the female holotype of *turpiter* but is identical in color patterns and male genitalia to the male allotype of *nigridens*, which is treated as a junior synonym of *albocinctus* in this paper.

From *anademus*, to which it is similar in general habitus, *clathrus* can be separated




Figs. 64–68. *Colladonus clathrus* (DeLong): 64, male pygofer, lateral view; 65, connective and right style, dorsal view; 66, aedeagus, lateral view; 67, apex of right style, enlarged dorsal view; 68, apex of aedeagus and distal processes, enlarged dorsal view.

from all known Mexican and Central American species by the reflexed, distal, bifurcated aedeagal processes.

### *Colladonus beameri* (Ball)

Figs. 69–75

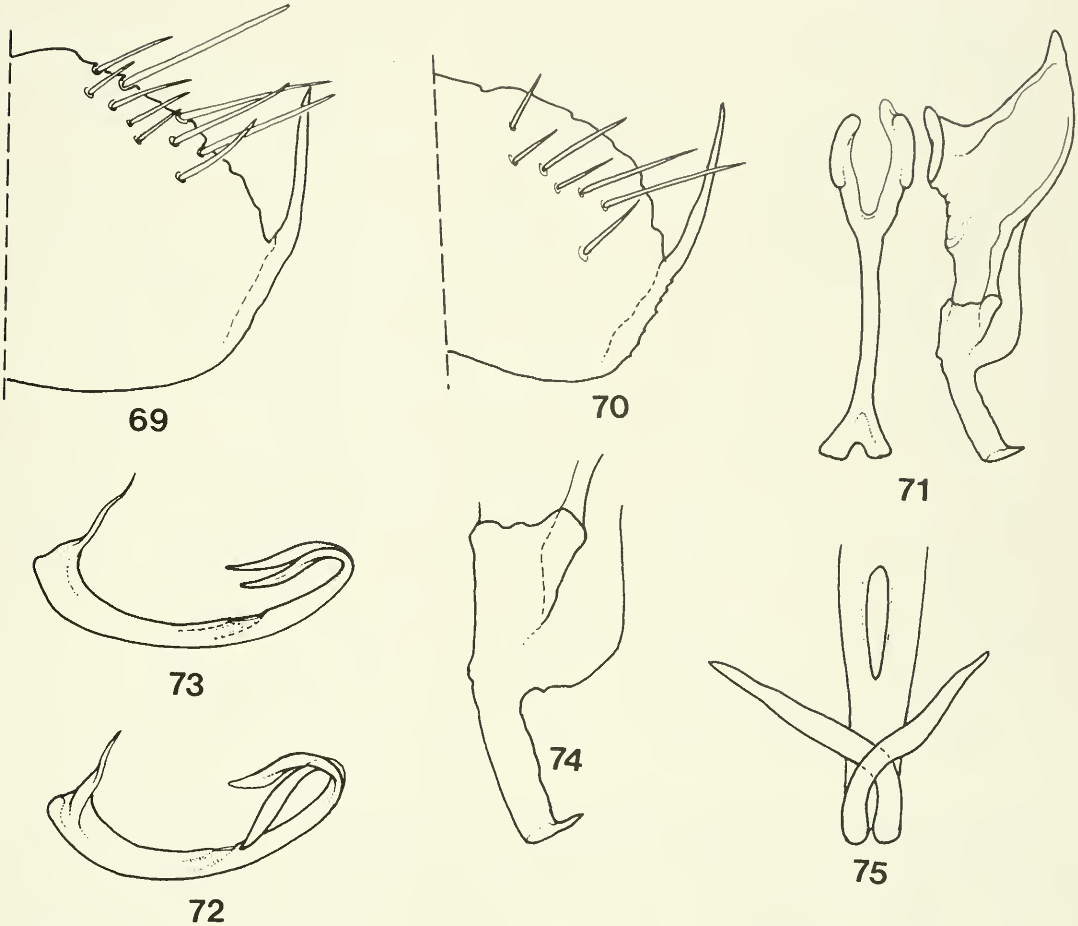
*Idiodonus beameri:* Ball 1937:28 [Holotype ♀ (USNM) (examined).]
*Idiodonus beameri:* DeLong 1946:17
*Colladonus beameri:* Oman 1949:125
*Colladonus beameri:* Nielson 1957:45
*Colladonus beameri:* Metcalf 1967:1244
*Idiodonus beamerellus:* DeLong 1983:92 [Invalid replacement name for nonexistent species, *Idiodonus beameri:* DeLong 1946:17 nec *Idiodonus beameri* Ball 1937:28.]
*Idiodonus beamerellus:* DeLong 1984:10
*Idiodonus marginatus:* DeLong 1983:90 [Holotype ♂ (OSU) (examined).] New synonymy
*Idiodonus marginatus:* DeLong 1984:10

LENGTH.—Male, 4.2–4.6 mm; female, 5.0–5.3 mm.

General color tawny throughout with black spots along anterior margin of crown, spots sometimes numbering as many as eight, four on anterior margin and two each above and below margin next to eye, spots sometimes connected. Similar in general habitus to *incidus* (DeLong) but larger and with additional spots on crown and distinctive male genitalia.

Head with anterior margin not produced, apex rounded.

MALE.—Pygofer in lateral view with very



Figs. 69–75. *Colladonus beameri* (Ball): 69, male pygofer, lateral view; 70, male pygofer (holotype of *marginatus*), lateral view; 71, connective and right style, dorsal view; 72, aedeagus, lateral view; 73, aedeagus (holotype of *marginatus*), lateral view; 74, apex of right style, enlarged dorsal view; 75, apex of aedeagus and distal processes, enlarged dorsal view.

long spine, exposed length about as long as fused basal half (Figs. 69, 70); aedeagus in lateral view with short, bifurcated distal processes, processes reaching to gonopore (Fig. 72, 73), crossing over in dorsal view (Fig. 75), gonopore distad of middle of shaft; connective long, extending to or slightly beyond apex of style (Fig. 71); style with long stylar shaft, lateral margins smooth, stylar spine very short and projecting laterally (Fig. 74).

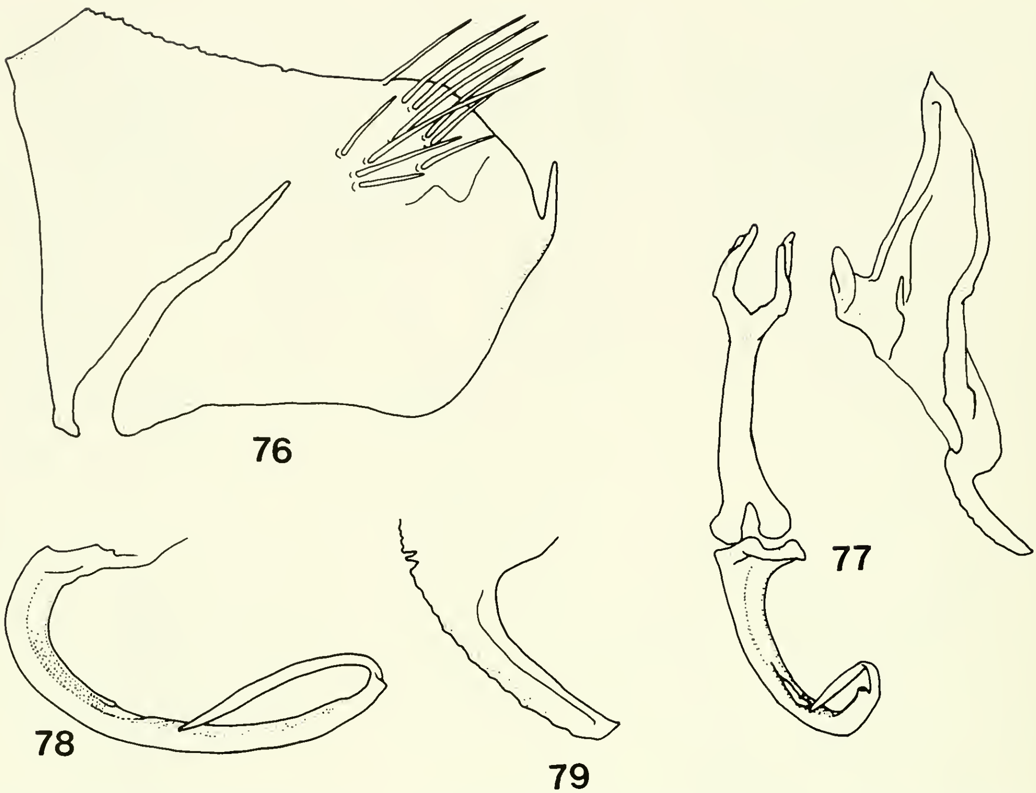
FEMALE.—Seventh sternum with subtruncate caudal margin, with shallow, V-shaped emargination medially.

DISTRIBUTION.—This is a widespread species known from the Mexican states of Michoacán, Distrito Federal, Puebla, Hidalgo, Veracruz, Jalisco, and Morelos, and from the state of Arizona.

HOST.—Specimens were collected from pine at elevations from 5,500 to 9,800 feet during October in Mexico (DeLong 1946)

REMARKS.—DeLong (1983) proposed *beamerellus* as a replacement name for his supposed "*beameri* Delong" treated as *beameri* Ball in his 1946 paper. That action was actually based on a nonexistent species.

The male holotype of *marginatus* is identical to authentically determined males of *beameri*. From *incidus*, to which it is similar in general habitus, *beameri* can be distinguished by the eight spots on the anterior margin of the crown and by the very long pygofer spine.




Figs. 76–79. *Colladonus tessellatus*, n. sp.: 76, male pygofer, lateral view; 77, connective, right style, and aedeagus, dorsal view; 78, aedeagus, lateral view; 79, apex of right style, enlarged dorsal view.

*Colladonus tessellatus*, n. sp.
Figs. 76–79

LENGTH.—Male, 4.3 mm; female, 4.7–4.9 mm.

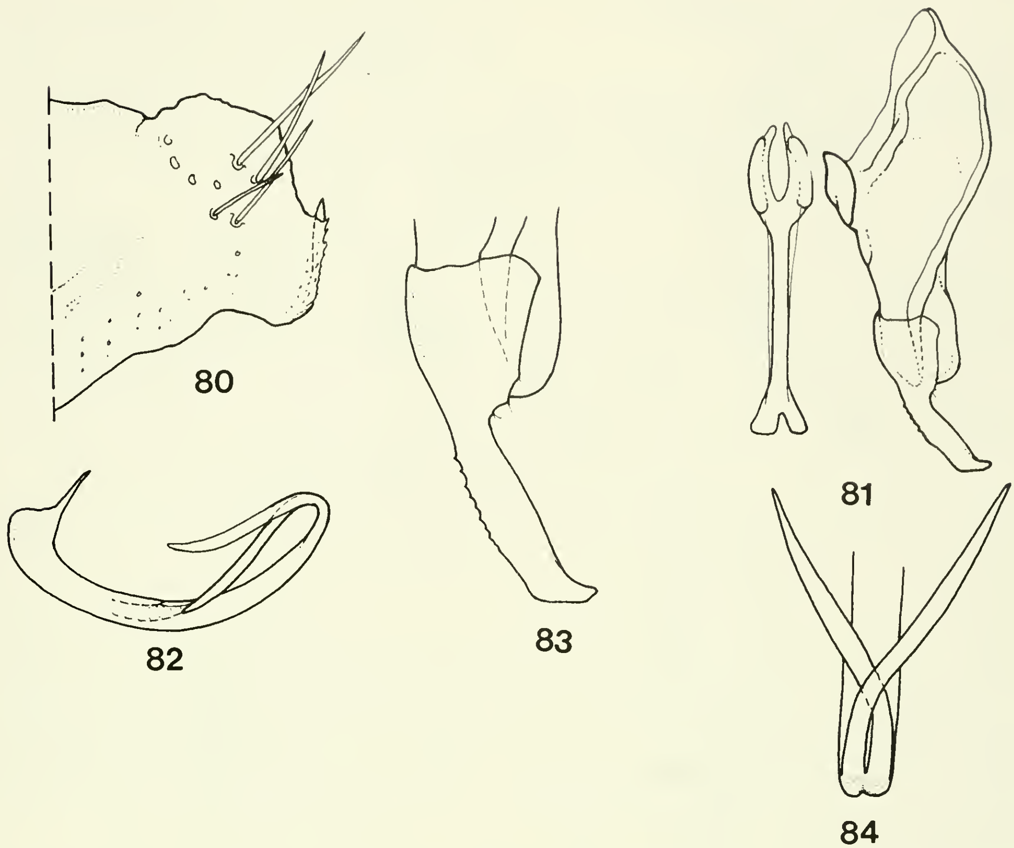
Color tan to tannish brown with dark brown markings on dorsum; crown with two large, subquadrate spots on anterior margin, small spot in ocellocular area next to lateral frontal suture, two large spots on disc separated widely at middle; pronotum with dark, mosaic markings separated by narrow, tannish line medially; forewings with dark markings in cells, veins mostly tannish to yellow tannish; face tan with dark markings. Similar to *trabilis* in male genitalic characters.

Head with anterior margin produced, apex rounded.

MALE.—Pygofer in lateral view with caudal margin obtusely angled, pygofer spine moderately long, arising at apex of caudal margin above middle and slightly curved dorsad (Fig. 76); aedeagus in lateral view narrow along major portion of shaft, with moderately long, distal, bifurcated process (one process broken off in holotype) (Fig. 78) reaching to about midlength of shaft, gonopore basad of midlength of shaft; connective short, not reaching apex of style (Fig. 77); style with narrow stylar shaft, inner lateral margin serrate, slightly tapered distally and curved laterad, stylar spine very small (Fig. 79).

FEMALE.—Seventh sternum with truncate caudal margin, very small, shallow excavation medially.

HOLOTYPE (male).—MEXICO: Mex. D.F., 5 mi west of Tlamacas, P.N. Ixtapopo, 10,000 ft, 31.V.1974, C. W. and L. O'Brien and Marshall (BYU), female allotype, same data as holotype (BYU). Paratypes: one male and one female, same data as holotype (author's collection); three females, same data as holotype (BYU); one female, 11 mi east of Amecameca, 10,300 ft, 31.V.1974, C. S. and L. O'Brien and Marshall; one female, P.N., Cumbres de




Figs. 80–84. *Colladonus anademus* (DeLong): 82, male pygofer, lateral view; 81, connective and right style, dorsal view; 82, aedeagus, lateral view; 83, apex of right style, enlarged dorsal view; 84, apex of aedeagus and distal processes, enlarged dorsal view.

Ajusco, Llano de Cantimplora, 3,340 m, 4.IX.1982, C. W. and L. B. O'Brien and G. J. Wibmer (CAS).

REMARKS.—From *trabilis*, to which it is similar in certain male genitalic features, *tessellatus* can be separated by the gonopore, which is basad of midlength of the aedeagal shaft, by the short connective, and by the slender stylar shaft, which is serrate on the inner lateral margin.

### *Colladonus anademus* (DeLong)

Figs. 80–84

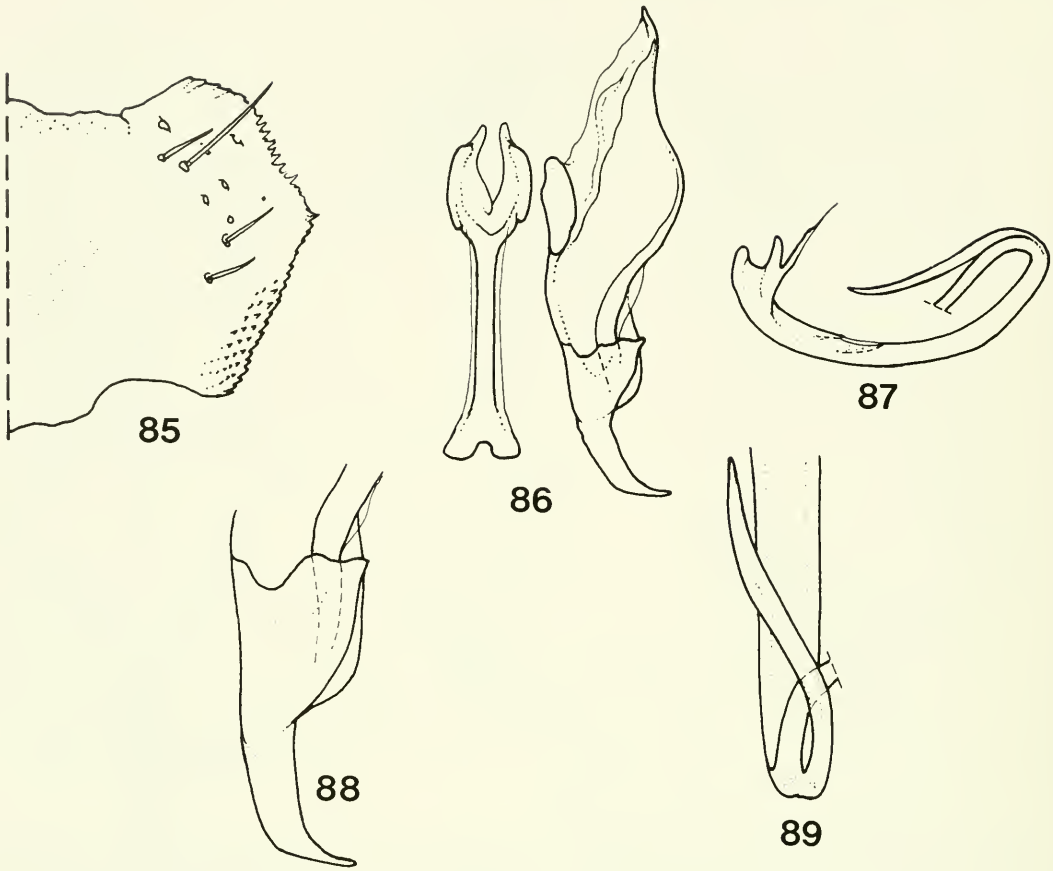
*Idiodonus anademus* DeLong 1946:29 [Holotype ♀ (OSU) (examined).]
*Colladonus anademus:* Nielson 1957:51
*Idiodonus anademus:* Metcalf 1967:1286
*Idiodonus anademus:* DeLong 1983:90
*Idiodonus anademus:* DeLong 1984:10

LENGTH.—Male, 4.8 mm; female, 4.9–5.1 mm.

General color tawny throughout with two distinct, black, elongate, triangular spots on anterior margin of crown, small black markings on disc of crown and pronotum. Similar in general habitus to *incidus* (DeLong) but with distinctive male genitalia.

Head with anterior margin not produced, apex rounded.

MALE.—Pygofer in lateral view with caudoventral margin produced distally, subtruncate and serrate (Fig. 80), pygofer spine very short, basal 3/4 sclerotized and fused to inner mesal margin of pygofer, spine projecting dorsad (Fig. 80); aedeagus in lateral view with slender, distal, bifurcated processes reaching to midlength of shaft (Fig. 82), crossing over in dorsal view (Fig. 84), gonopore at about middle of shaft; connective long, nearly reaching to apex of style (Fig. 81); style with long, narrow stylar shaft, inner lateral margin




Figs. 85–89. *Colladonus incidus:* 85, male pygofer, lateral view; 86, connective and right style, dorsal view; 87, aedeagus, lateral view; 88, apex of right style, enlarged lateral view; 89, apex of aedeagus and distal processes, enlarged dorsal view.

serrate, outer one smooth, stylar spine short, blunt, and directed laterad.

FEMALE.—Seventh sternum with caudal margin convex, shallow, narrow, V-shaped excision medially.

HOST.—Specimens were collected on pine by DeLong (1946).

DISTRIBUTION.—This species is known only from the Mexican state of Distrito Federal.

REMARKS.—The female holotype and male allotype appear to be correctly associated. This species, similar to *incidus*, can be distinguished by the produced, subtruncate caudoventral margin of the pygofer, by the short, dorsally directed pygofer spine, and by the long, narrow stylar shaft.

*Colladonus incidus* (DeLong), n. comb.
Figs. 85–89

*Idiodonus incidus* DeLong 1946:29 [Holotype ♀ (OSU) (examined).]
*Idiodonus incidus:* Metcalf 1967:1299
*Idiodonus incidus* DeLong 1984:11
*Idiodonus pallidus:* DeLong 1983:90 [Holotype ♂ (OSU) (examined).] New synonymy
*Idiodonus pallidus:* DeLong 1984:10

LENGTH.—Male, 4.8 mm; female, 4.9–5.1 mm.

General color tawny throughout with two small, black spots on anterior margin of crown. Similar in general habitus to *anademus* but with distinctive male genitalia.

Head with anterior margin produced, apex angled.

MALE.—Pygofer in lateral view with broadly angled, serrate caudal margin, very small spine at middle of margin, spine directed distad (Fig. 85); aedeagus with slender, distal, bifurcated processes extending beyond midlength of shaft (Fig. 87), crossing over in

dorsal view (Fig. 89), gonopore at midlength of shaft; connective short, not reaching to apex of style (Fig. 86); style with slender stylar shaft, lateral margins smooth, stylar spine long, directed laterad (Fig. 88).

FEMALE.—Seventh sternum with broadly convex caudal margin, very small indentation medially.

DISTRIBUTION.—This species is known only from the Mexican state of Distrito Federal.

HOST.—Specimens were collected from unspecified trees or shrubs at 8,500 feet during September and October in Mexico (DeLong 1946).

REMARKS.—No males of *incidus* were described in the type series. The female holotype of *incidus* was associated with the male holotype of *pallidus* and is identical with the female allotype of *pallidus*. The latter name is the more recent and is, therefore, suppressed as a junior synonym of *incidus*.

From *anademus*, to which it is similar, *incidus* can be easily separated by the serrated, broadly angled caudal margin of the pygofer with its very small, distally directed spine, by the shorter connective, and by the longer, distal, bifurcated processes of the aedeagus.

## *Paracolladonus*, new genus

TYPE-SPECIES: *Idiodonus insculptus* DeLong 1946:25.

Similar to *Colladonus* Ball and *Dolyobius* Linnavuori in general habitus but with distinctive male genitalia. General color tannish brown in female to black in male with dark markings on crown, pronotum, and scutellum.

Head slightly wider than pronotum, anterior margin broadly rounded and slightly produced medially; pronotum with posterior margin broadly concave; scutellum as in *Colladonus*; clypeus broad anteriorly; venation of forewing similar to *Colladonus*, inner anteapical open basally.

Male pygofer with large spine on caudoventral margin, setose caudodorsally; aedeagus long, broadly recurved, somewhat compressed dorsoventrally, with paired, recurved, short, distal processes, processes sometimes with secondary process medially, gonopore subapical on dorsal surface; connective long and narrow; style broad at basal half, with foot-shaped apex.

### *Paracolladonus insculptus* (DeLong), n. comb.

Figs. 90–94

*Idiodonus insculptus:* DeLong 1946:25 [Holotype ♀ (OSU) (examined).]
*Idiodonus insculptus:* Metcalf 1967:1299
*Idiodonus insculptus:* DeLong 1984:11

LENGTH.—Male, 5.3 mm; female, 5.7–5.9 mm.

Long, slender species with dark markings on crown, pronotum, and scutellum; pronotum black in male, light brown in female with dark markings on anterior margin; forewing light to dark brown with yellowish veins.

Male pygofer with very long, stout spine on caudoventral margin, spine projecting caudodorsad, numerous setae confined to caudodorsal area (Fig. 90), aedeagus in lateral view long, recurved, with distal processes short, broad medially (Fig. 92), sometimes with secondary process medially (Fig. 94) (if absent, basal attachment apparent in dorsal view), curved dorsad in lateral view, slightly flared laterally in dorsal view (Fig. 93), shaft somewhat flattened dorsoventrally (Fig. 94), gonopore subapical on dorsal surface; connective long and narrow, reaching to or beyond apex of style (Fig. 91); style with narrow ridge or flange from inner lateral margin above preapical lobe to apex of style in dorsal view (Fig. 92).

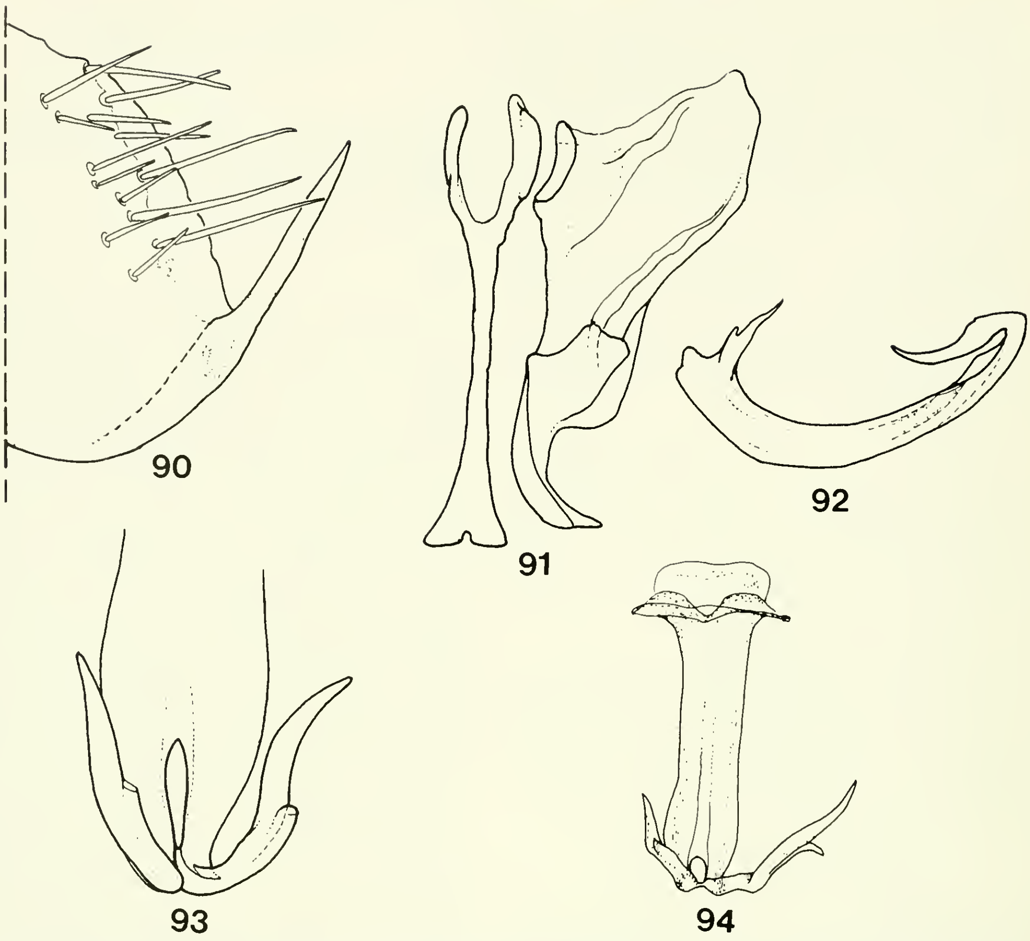
REMARKS.—This is the only known species assigned to the genus. It is known from the states of Distrito Federal and Morelos in Mexico. DeLong (1946) collected specimens from pine at 10,000 feet in September and October. A pair of specimens were collected on the Cuernavaca road in Mexico by Ball and Stone.

## *Paranurenus*, new genus

TYPE-SPECIES: *Idiodonus latidens* DeLong 1946:26

Similar to *Colladonus* in general habitus and *Nurenus* in some male genital characters. General color tawny with black markings on head. Pronotum with ivory, transverse band, forewings with ivory stripe on claval suture.

Head about as wide as pronotum; crown produced, longer medially than next to eye; pronotum and scutellum as in *Colladonus*; forewing as in *Colladonus*; venation partially obscured; clypeus long; clypellus long and narrow.




Figs. 90–94. *Paracolladonus insculptus* (DeLong): 90, male pygofer, lateral view; 91, connective and right style, dorsal view; 92, aedeagus, lateral view (allotype); 93, aedeagus, enlarged dorsal view (allotype); 94, aedeagus, dorsal view (specimen from Cuernavaca Road, Mex.).

Male pygofer without caudal spine, margin obliquely truncate as in *Nurenus;* aedeagus small, recurved, flattened dorsoventrally with pair of short, acuminate distal processes; gonopore subapical on dorsal surface; connective and style as in *Colladonus.*

*Paranurenus* is represented by a single known species from Mexico.

From *Colladonus,* to which it is similar in general habitus, *Paranurenus* can easily be differentiated by the flattened aedeagus and by the absence of a pygofer spine. The head characters and the flattened shaft of the aedeagus will differentiate the genus from *Nurenus.*

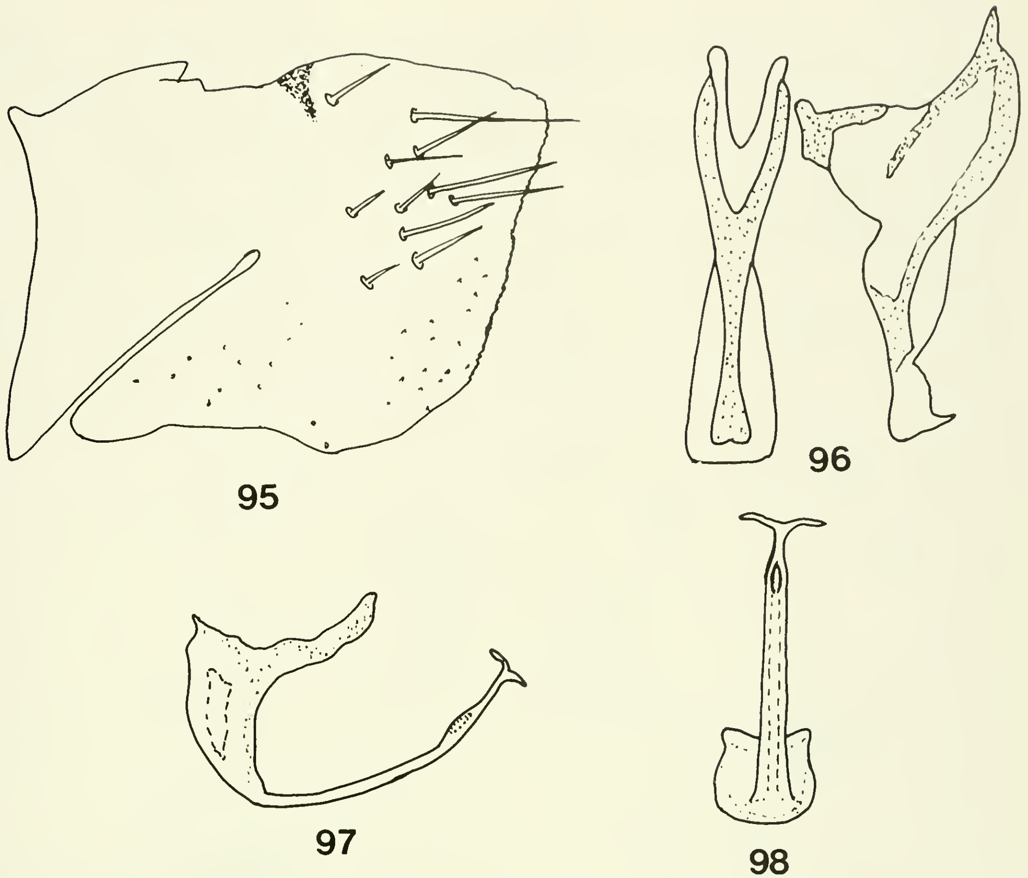
*Paranurenus latidens* (DeLong), n. comb.
Figs. 95–98

*Idiodonus latidens:* DeLong 1945:26 [Holotype ♀ (OSU) (examined).]
*Idiodonus latidens:* Metcalf 1967:1300
*Idiodonus latidens* DeLong 1984:11

LENGTH.—Male, 4.4–4.5 mm; female, 4.8–5.1 mm.

Color tawny, crown ivory with two black spots on anterior margin and narrow, black, transverse band on disc between eyes; pronotum tawny with narrow, ivory, transverse band above middle; scutellum tawny; forewing tawny with ivory on claval suture extending to pronotal band, fuscous band above costal area; face ivory to tawny with black markings.

MALE.—Pygofer in lateral view with obliquely truncate caudal margin, pygofer spine absent, macrosetae on caudodorsal quadrant (Fig. 95); aedeagus in lateral view recurved, socle large, shaft slender, flattened



Figs. 95–98. *Paranurenus latidens* (DeLong): 95, male pygofer, lateral view; 96, connective and right style, dorsal view; 97, aedeagus, lateral view; 98, aedeagus, ventral view.

dorsoventrally (Fig. 97) with pair of short, acuminate distal processes, processes directed laterad in ventral view (Fig. 98); gonopore subapical on dorsal surface of shaft; connective long and narrow, extending just beyond apex of style (Fig. 96); style with stylar shaft short and enlarged distally, stylar spine prominent, subapical, and projecting laterally (Fig. 96).

FEMALE.—Seventh sternum with short, median, spatulate process on caudal margin.

REMARKS.—This species has no known close relatives. The styles are typical of many species of *Colladonus*, and the aedeagus, except for its flattened condition, is similar in configuration to *Nurenus*. The head characters and general habitus are similar to species of *Colladonus*.

The species is known from the states of Michoacán and Distrito Federal in Mexico, and occur at elevations from 5,000 to 8,000 feet in February and September on unspecified shrubs or trees (DeLong 1946).

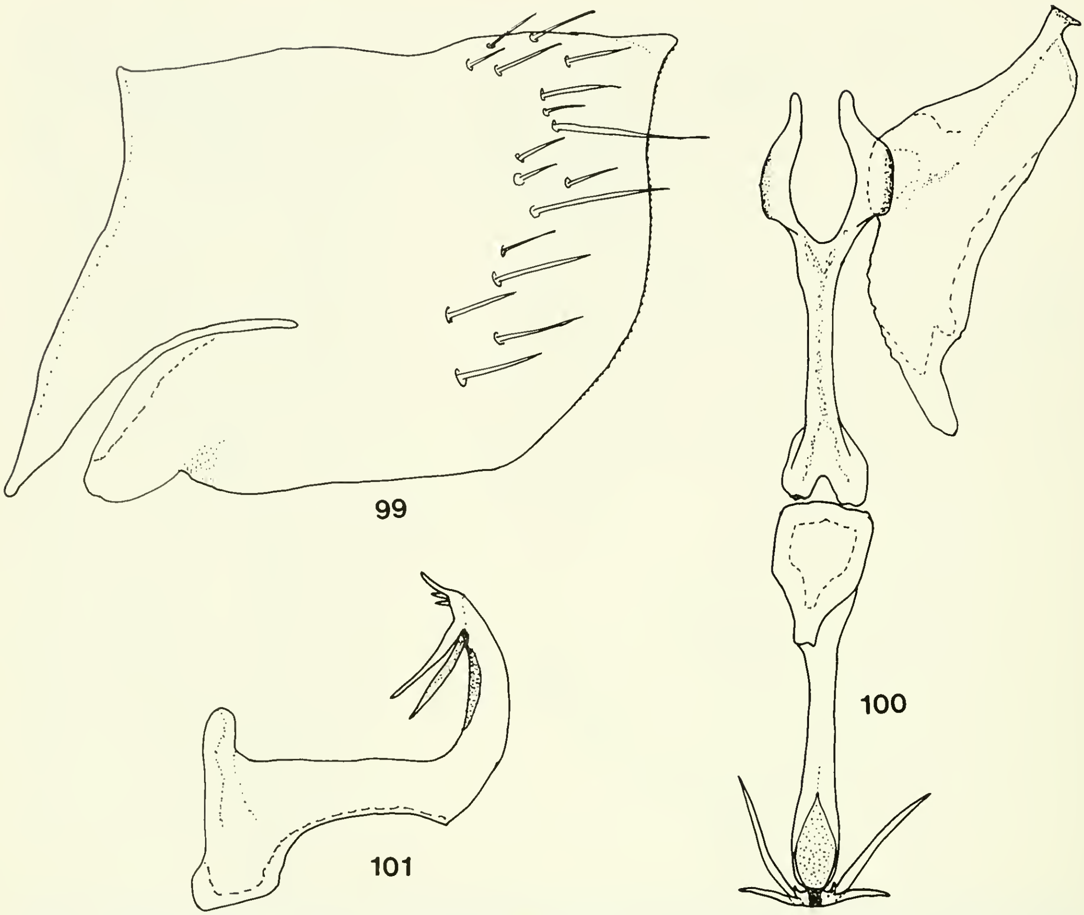
## *Jaacunga*, new genus

TYPE-SPECIES: *Idiodonus vinculus* DeLong 1945:15

Similar to *Paracolladonus* in general habitus but more robust with slightly wider head and distinctive male genitalia. General color tawny with markings on crown, narrow band on pronotum and iridescent forewings.

Head wider than pronotum, anterior margin broadly rounded and slightly produced as in *Paracolladonus;* pronotum large, posterior margin broadly and shallowly concave; forewing venation as in *Paracolladonus*.

Male pygofer without caudal spine, setose submarginally; aedeagus stout with enlarged socle, recurved at apical third with terminal




Figs. 99–101. *Jaacunga vinculus* (DeLong): 99, male pygofer, lateral view; 100, connective, right style, and aedeagus, dorsal view; 101, aedeagus, lateral view.

processes, gonopore large, subapical on dorsal surface; connective Y-shaped; style without apical spine. Female seventh sternum with median spatulate process. Two species, described below, are assigned to the genus.

*Jaacunga vinculus* (DeLong), n. comb.
Figs. 99–101

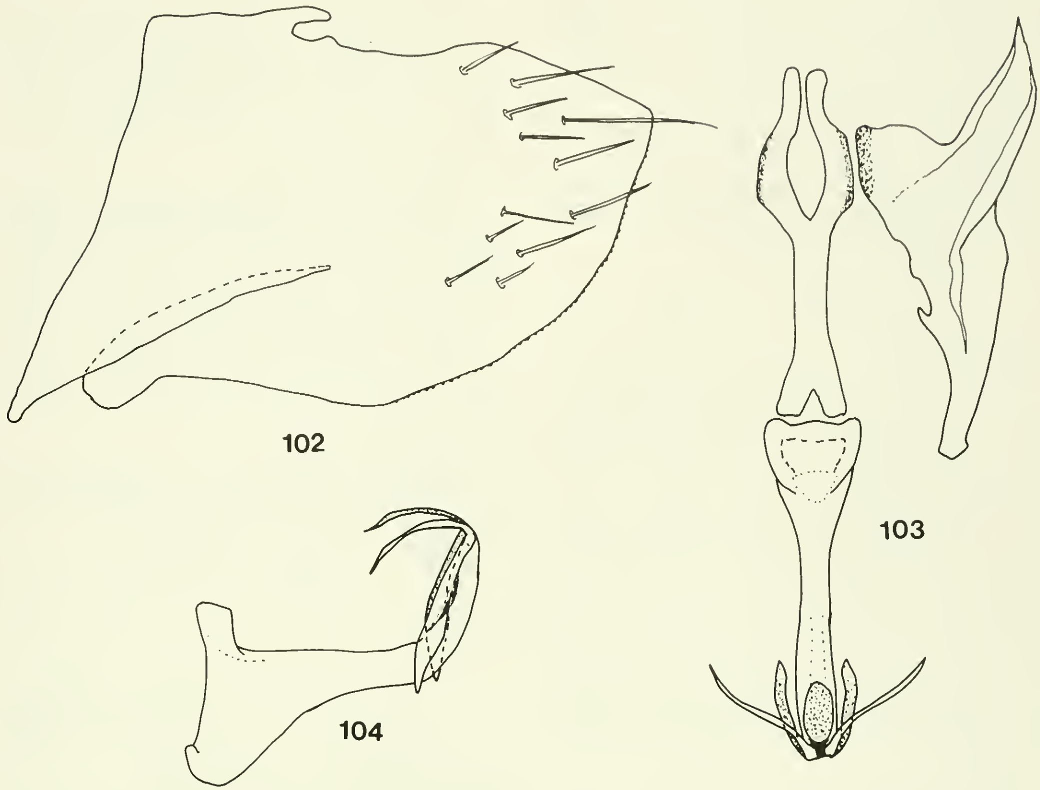
*Idiodonus vinculus:* DeLong 1946:15 [Holotype ♀ (OSU) (examined).]
*Idiodonus vinculus:* Metcalf 1967:1304
*Idiodonus vinculus* DeLong, 1984:10

LENGTH.—Male, 5.8 mm; female, 6.4 mm.

Long, robust species with two spots on anterior margin of crown and narrow, black, transverse, irregular band on disc in male, less marked in female; pronotum with narrow, yellow or ivory, transverse band near middle and similar, less pronounced band on posterior margin; forewing iridescent, veins black to tawny. Similar to *spatulatus* in male genital character.

MALE.—Pygofer without caudal spine, macrosetae on submargin from dorsal to ventral margin (Fig. 99); aedeagus in lateral view stout, socle enlarged, shaft tubular, curved dorsad at apical half with six terminal spines, two long and projecting anteroventrally, two moderately long and projecting anterodorsad, and two very short and projecting anteriorly (Fig. 101), gonopore large, subapical on dorsal surface; connective stout, Y-shaped, extending slightly beyond apex of style (Fig. 100); style similar to *Colladonus* but broader at basal two-thirds, stylar apex narrow, without distinct stylar spine, apex obliquely truncate.

FEMALE.—Seventh sternum with short, apically bifid, medial projection on caudal margin, shallowly excavated on either side of projection.




Figs. 102–104. *Jaacunga spatulatus* (DeLong): 102, male pygofer, lateral view; 103, connective, right style, and aedeagus, dorsal view; 104, aedeagus, lateral view.

REMARKS.—This species is known from the female holotype and male allotype specimens collected at Jacala, Hidalgo, Mexico, and Acapulco Road, Mexico, respectively. Other specimens that I have not seen are reported from Mexico City and Jalapa Road in Mexico by DeLong (1946). All specimens were collected from September to October at elevations from 5,000 to 8,500 feet from unspecified shrubs or trees.

*Jaacunga vinculus* can be distinguished from *spatulatus* by its six terminal spines, which differ in their configuration, and by the shape of the apex of the style.

### *Jaacunga spatulatus* (DeLong), n. comb.

Figs. 102–104

*Idiodonus spatulatus* DeLong 1946:15 [Holotype ♀ (OSU) (examined).]
*Idiodonus spatulatus:* Metcalf 1967:1302
*Idiodonus spatulatus* DeLong 1984:10
*Idiodonus rubellus* DeLong 1946:15 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus rubellus:* Metcalf 1967:1301
*Idiodonus rubellus* DeLong 1984:9

LENGTH.—Male, 5.5 mm; female, 5.5–5.8 mm.

Similar in general habitus to *vinculus* but with distinctive male genitalia.

Male pygofer without caudal spine, macrosetae submarginal in caudodorsal area (Fig. 102); aedeagus in lateral view stout but not as robust as in *vinculus*, socle enlarged, shaft similar to *vinculus*, with four terminal processes, longest pair projecting ventrally and broad before gradually pointed apex, second pair shorter, projecting anteriorly with tips curved ventrally (Figs. 103, 104); gonopore large, subapical on dorsal surface; connective similar to *vinculus* except shorter, not reaching apex of style (Fig. 103); style as in *vinculus* except apex curved mesally and rounded distally.

REMARKS.—*Jaacunga spatulatus* is known from the type series collected from Mexico City and from the female holotype of *rubellus*, which has the same type locality as *spatulatus*. The specimens were collected from unspecified shrubs at elevations of 7,500 to 8,500 feet in September (DeLong 1946). The species can be distinguished from *vinculus* by the shape of four terminal spines on the aedeagus and by the shape of the stylar apex.

## *Paracrassana*, new genus

TYPE-SPECIES: *Idiodonus nigrifrons* DeLong 1983:91

Near *Crassana* DeLong & Heishberger but with distinctive head, facial, and genitalic features. General color tawny with black markings on head and thorax, face black.

Head slightly wider than pronotum, anterior margin slightly angled and produced medially, not rounded to face, clearly demarcated but not carinate, narrow, transverse impression submarginally between ocelli, surface shiny, striate longitudinally; ocellus remote from eye; forewing as in *Crassana;* clypeus broad anteriorly, about as wide as long; clypellus long, lateral margins expanded distally.

Male pygofer long, with deep incision basally to near middle, dorsal margin broadly excavated near middle, row of fine teeth on ventral margin; aedeagus symmetrical, long, narrow, nearly tubelike, socle basal, gonopore terminal, sclerotized endotheca basad of aedeagal shaft; connective very short as in *Crassana* and *Neocrassana* Linnavuori; plate long, triangular, tenth segment sclerotized laterally.

*Paracrassana* is represented by a single known species from Mexico. It can be distinguished from *Crassana* by the narrow demarcation between the crown and face, the narrow impression submarginally on the crown, the long pygofer with basal incision and tubular aedeagus. From *Neocrassana*, it can be distinguished by the remote position of the ocelli from eyes, the position of the socle on the aedeagus, and characters described above.

### *Paracrassana nigrifrons* (DeLong), n. comb.
Figs. 105–107

*Idiodonus nigrifrons* DeLong 1983:91 [Holotype ♂ (OSU) (examined).]

LENGTH.—Male, 5.4 mm.

Long, robust species, crown with irregular, narrow, black, transverse band between ocelli; pronotum with black markings on anterior lateral angles; face black except for narrow, yellow anterior margin; forewing iridescent, veins fuscous.

Male pygofer in lateral view long and narrow, macrosetae on distal third except caudal margin, ventral margin with fine spines (Fig. 105); aedeagus long, tubular, curved dorsally at distal third, with subdistal flange laterally on dorsal margin (Fig. 106), gonopore apical, endotheca not forming a loop; connective short, broad; style narrow, with narrowed curved apices.

FEMALE.—Unknown.

REMARKS.—This species is known only from the male holotype from Huanchinango, Puebla, Mexico. The host is unknown.

The nomenclature of a few species described in *Idiodonus* and *Colladonus* are treated below:

### *Bonneyana caldwelli* (DeLong), n. comb.

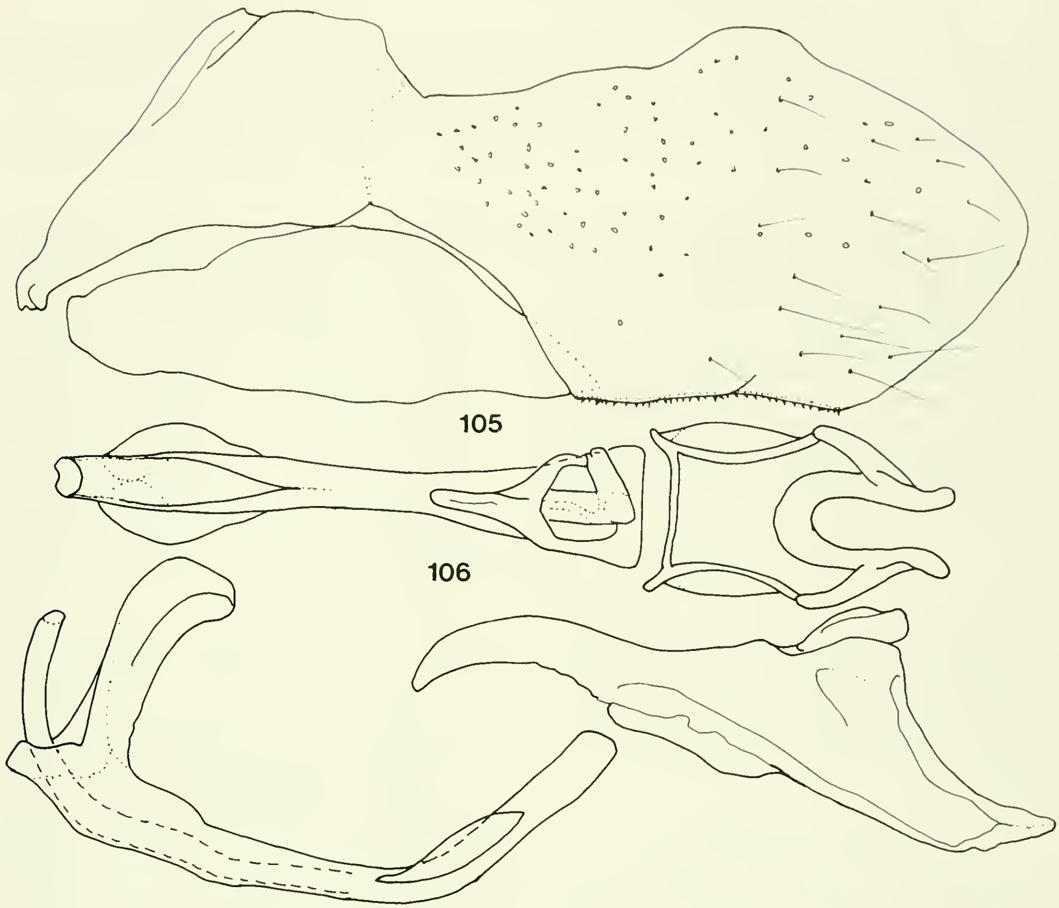
*Idiodonus caldwelli* DeLong 1946:16 [Holotype ♀ (OSU) (examined).]
*Idiodonus caldwelli:* Metcalf 1967:1288
*Idiodonus caldwelli* DeLong, 1984:10
*Idiodonus apertus* DeLong 1946:14 [Holotype ♀ (OSU) (examined).] New synonymy.
*Idiodonus apertus:* Metcalf 1967:1287
*Idiodonus apertus* Delong 1984:10

I have compared dissected specimens of *caldwelli* and *schwartzi* (Ball) and found them to be distinct. Two remaining known species in the genus, *osborni* (Ball) and *terminalis* (Ball), have not been examined; but, based on the original descriptions, they appear to be distinct from *caldwelli*. Further study of the group is warranted, however, including illustrations and descriptions of the male diagnostic characters.

### *Ollarianus tripartitus* DeLong

*Ollarianus tripartitus* DeLong 1944:398
*Idiodonus albifrons* DeLong 1983:89 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus albifrons* DeLong 1984:10

Examination of the female holotype of *I. albifrons* and comparison with specimens of several species of *Ollarianus* show that it belongs in that genus and is identical with *O. tripartitus*. The genus *Ollarianus* has wide




Figs. 105–107. *Paracrassana nigrifrons* (DeLong): 105, male pygofer, lateral view; 106, connective, right style, and aedeagus, dorsal view; 107, aedeagus, lateral view.

distribution from the Nearctic to the Neotropical region and needs revision.

*Paratanus costatus* (DeLong), n. comb.

*Idiodonus costatus* DeLong 1984:92 [Holotype ♂ (OSU) (examined).]

This species is close to *Paratanus wygodzinskyi recurvatus* (Linnavuori) but differs from it in color characters. It may be a distinct subspecies of the nominate form or a separate species pending studies of the genus *Paratanus.*

*Angulanus* DeLong, n. status

*Idiodonus* subgenus *Angulanus* DeLong 1946:30. Type-species, *Idiodonus incisurus* DeLong 1946:30. [Holotype ♀ (OSU) (examined).]
*Idiodonus (Angulanus):* Metcalf 1967:1304
*Idiodonus:* DeLong 1984:9. [Inadvertent synonymy of *Angulanus* DeLong in the treatment of the type-species, *incisurus* DeLong, in a key to the species of *Idiodonus*.]

Examination of the genital structures of the male allotype clearly showed that *Angulanus* deserves generic-level rank. The aedeagus is asymmetrical, and the pygofer possesses a prominent spine on the caudal margin, characters that are not descriptive of the genus *Idiodonus.*

*Angulanus incisurus* (DeLong), n. comb.

*Idiodonus incisurus* DeLong 1946:30 [Holotype ♀ (OSU) (examined).]
*Idiodonus incisurus:* DeLong 1946:13, 14
*Idiodonus (Angulanus) incisurus:* Metcalf 1967:1304
*Idiodonus (Angulanus) incisurus:* DeLong 1984:10

### *Idiodonus plummeri* DeLong

*Idiodonus plummeri* DeLong 1946:25 [Holotype ♀ (OSU) (examined).]
*Idiodonus plummeri:* DeLong 1984:11
*Idiodonus bakeri:* DeLong 1984:26 [Holotype ♀ (OSU) (examined).] New synonymy
*Idiodonus bakeri:* DeLong 1984:11

The generic placement of this species appears to be correct. No males were described in the type series of *plummeri* or *bakeri*, but a male paratype specimen labeled "*Idiodonus bakeri* DeLong, MB 73, Mexico, A. Dampf coll." was found and examined. The genitalic structures clearly show that it belongs in *Idiodonus*. The species was associated with the female holotype of *bakeri*, which was found to be identical with the female holotype of *plummeri*.

### Species *incertae sedis*

Three species of *Idiodonus* described by DeLong, *edentulus*, *excavatus*, and *copulus*, are treated herein as *incertae sedis* until males are known and associated with females of these species. *Idiodonus copulus* appears to be close to *Jaacunga* and may belong in that genus.

## ACKNOWLEDGMENTS

I thank Dr. Charles A. Triplehorn and Dr. Paul Cwikla, Ohio State University (OSU), for placing on loan nearly the entire type series of all the *Idiodonus* species from Mexico and Central America described by the late Dr. D. M. DeLong. Without this material it would not have been possible to unravel the taxonomic problems involved with the *Idiodonus* and *Colladonus* fauna in that part of the world. I also thank Dr. James P. Kramer, U.S. National Museum, for the loan of the type of *Colladonus delongi* Linnavuori and material of genera related to *Colladonus*.

My appreciation is extended to Jeanette Price and Pamela Scott for the illustrations and to Kaye Thorne for identifying the host plant of a population of the *Colladonus belli* complex. I thank Dr. Leon Hepner for reading the manuscript and offering helpful suggestions to improve its content.

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# NEW WORLD FULGORIDAE, PART I: GENERA WITH ELONGATE HEAD PROCESSES

Lois B. O'Brien[1]

ABSTRACT.—Genera new to science described below include: *Amerzanna*, *Sinuala*, and *Stalubra*. New species include: *Amerzanna peruana* (Peru), *Amycle brevis* (Mexico), *A. grandis* (Mexico), *A. mankinsi* (Honduras), *Aphrodisias shaman* (Mexico), *Enchophora maculata* and *E. uniformis* (Peru), *Phrictus delicatus* (Brazil), *P. diligens* (Colombia), *Sinuala schmidti* (Belize), *S. stali* (Honduras and El Salvador), *S. tuberculata* (Costa Rica), and *Stalubra brunnea* (Brazil and Guyana). In addition, *Artacie dufourii* (Signoret) is removed from synonymy with *A. haemoptera* (Perty). New generic synonymy includes *Chilobia* Stål (= Ecuadoria) Distant, *Enhydria* (Walker) (= *Ulubra* Stål). New synonymy of species includes: *Copidocephala merula* Distant (= *Coanaco melanoptera* Schmidt), *Copidocephala viridiguttata* Stål (= *Coanaco ornanda* Distant), *Diareusa conspersa* Schmidt (= *D. dahli* Ossiannilsson), *Enchophora nigromaculata* Distant (= *E. nigrolimbata* Lallemand), *Enchophora recurva* (Olivier) (= *E. bohemani* Stål), *Enchophora sanguinea* Distant (= *E. florens* Distant and *E. longirostris* Distant), *Enchophora tuberculata* (Olivier) (= *E. parvipennis* Walker), *Enchophora viridipennis* Spinola (= *E. eminenta* Schmidt), *Enhydria tessellata* (Walker) (= *E. brachialis* Stål), *Fulgora graciliceps* Blanchard (= *Laternaria orthocephala* Fonseca), *Fulgora laternaria* (Linnaeus) (= *F. servillei* Spinola), *Phrictus auromaculatus* Distant (= *P. notatus* Lellemand), *Phrictus moebiusi* Schmidt (= *P. sordidus* Caldwell). The two species of *Fulgora* are synonymized by Ridout. New combinations include *Chilobia dichopteroides* (Distant) (*Ecuadoria*) and *Stalubra rufula* (Lallemand) (*Enhydria*).

Although the genera of New World Fulgoridae were monographed in an excellent paper by Stål (1870b), 25 of the 64 genera have been described since then. Also, there have been many subsequent species described, many in the wrong genus, and there are few keys to species. Consequently, even though they are large and beautiful insects, it is very difficult to identify most species. The purpose of this paper is to provide a guide for identification with emphasis on the use of external characters.

Very little is known about the biology of Fulgoridae. Two species have been reported to be of economic importance (Wilson and O'Brien 1987), *Phrictus diadema* (L.) on cocoa trees (*Theobroma cacao* L.) in Brazil (Silva 1945) and *Pyrops candelaria* (L.) on longan and mango (Kershaw and Kirkaldy 1910). Host records for species contained in this paper include *Amycle pinyonae* Knull & Knull on pinyon pine, *Pinus monophylla* Voss (Knull and Knull 1947), *Fulgora laternaria* (L.) on *Hymenaea courbaril* L. or quapinol (Janzen 1983), *Enchophora pallidipunctata* Lallemand on *Copaifera dourajeauni* (Leguminosae) (label data, species not found in botanical references), and *Rhabdocephala brunnea* Van Duzee on *Baccharis sarothroides* Gray. Johnson and Foster (1986) explored host specificity in a tropical forest, where plant diversity might make host finding difficult, and found 71% of *Enchophora longirostris* Distant (= *sanguinea* Distant) on *Simarouba amara* Aubl. (Sapindales) and 84% of *Phrictus quinquepartitus* Distant on *Terminalia oblonga* Steud. (Combretaceae). Adults have been reported to aggregate on tree trunks in ranks and to move in conjunction with each other (Johnson and Foster 1986, O'Brien and Wilson, 1985). Further host data will be given in parts to be published later.

Little information on life histories is available. Kershaw and Kirkaldy (1910) noted that the eggs of *Pyrops candelaria* were laid in flat clumps on tree trunks and covered with wax from the female abdominal segments; nymphs dispersed and fed on branches; and adults fed on tree trunks. Hingston (1932) reported rearing fulgorid nymphs from what he described as a mantidlike egg case. Other descriptions of immatures are those of *Fulgora phosphorea* L. (= *laternaria* L.) (Hagmann 1928); *Pristiopsis serratus* (F.) (= *Cathedra serrata* [F.]) (da Fonseca 1931), and *Itzalana submaculata* Schmidt (Wilson and O'Brien 1986). As far as

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is known, fulgorids feed in phloem tissue and are univoltine. No accounts of other typical fulgoroid behaviors, such as accoustical communication and association with ants, have been reported.

Fulgoridae are subject to predation by flycatchers (D. Wechsler, personal communication) and parasitization by the epipyropid moths (Lepidoptera, Epipyropidae). The colors of the closed wings would appear to make them inconspicuous against tree trunks, but they can be found fairly easily by the human eye if observed in profile. I assume that the red, orange, yellow, and white coloration so common at the base of the hind wings is similar in function to that of the underwing moths (Noctuidae), in which the color has been shown to startle birds seeking prey. Eye spots on the hind wings of *Cathedra* and *Fulgora* would seem to serve a startle or warning function as well. But for all the speculation on the bizarre shapes of the head processes, no one has reported the response of predators to the "alligator head" of the peanut bug, nor to any other species.

One common name for the family Fulgoridae, "lantern-flies," was given because *Fulgora* were reported to emit light (de Merian 1771), but recent inquiries and enzyme studies have failed to substantiate this phenomenon (Ridout 1983). Many Amerindians feared *Fulgora*, reporting that they flew a zigzag path through the forest, killing everything they touched (Branner 1885). Shamans carried one in their amulet bags. The modern version of this myth, probably invented and surely repeated in coed entomology classes far out in the bush, is that if a human is bitten by a *Fulgora*, death is certain unless one is saved by the antidote, mating within 24 hours; nonsense, of course.

Lallemand (1959, 1963) revised the 20 genera and 102 species of Fulgoridae from Africa and the 28 genera and 178 species of Asia and Australia. The New World has a much richer fauna, composed of 64 genera and 250 species as I begin this monograph. The only revisions of New World genera in which authors examined types are *Cyrpoptus* (Kramer 1978) and *Fulgora* (Ridout, personal communication). Other generic reviews are those on *Fulgora* (da Fonseca 1932), *Enchophora* (Metcalf 1938), *Phrictus* (Caldwell 1945), and *Poiocera* (Gerstaecker 1860), which are either out of date or relied on published descriptions. I have examined types of all but the following species: *Artacie dufourii* (Signoret) (MZF?, letter not answered); *A. haemoptera* (Perty) (ZSBS, not found); *Cathedra serrata* (Fabricius) (not listed by Zimsen 1964); *Copidocedphala melanoptera* Schmidt, *Diareusa conspersa* Schmidt, and *Enchophora eminenta* Schmidt (IZW); *Enchophora ensifera* (Germar) and *E. tuba* (Germar) (lost in Lvov, Russia); *E. nigrolimbata* Lallemand and *Enhydria rufula* Lallemand (FSAG, sent but not yet arrived); Olivier's species, *E. recurva*, *E. tuberculata*, and *F. caerulescens*, and the types of *Fulgora*, which were studied by Ridout. Olivier's (1791) species were redescriptions with Latin binomials of Stoll's (1781, 1788) descriptions and figures in French and Dutch or Flemish, using names in those languages. Olivier's species are not in the Paris Museum (MHNP), nor in his personal collection deposited there, which is all Coleoptera (Bourgoin, personal communication). Olivier cites "Du cabinet de M. Holthuisen" in some species; Horn and Kahle (1935) say of Holthuisen collection "in Hamburg am 3.II.1796 u. 16.V.1797 sowie in Stralsund 1800 verauktionert." If any specimens went to the Hamburg Museum (ZMUH), they were destroyed by bombing in World War II, except for a few specimens out on loan. I have not been able to trace Olivier's or Stoll's specimens further. The first three of the species listed here were well illustrated when described; Schmidt's descriptions clearly fit the specimens I have; only Lallemand's, Germar's, and Olivier's species are in doubt.

Fulgoridae may be distinguished from other Fulgoroidea by the presence of numerous cross-veins in the hind wings, a feature lacking in all other families. Stål also noted that the carina between the frons and gena continues onto the clypeus, but this feature also occurs in some Derbidae, Dictyopharidae, and Lophopidae. Fulgoridae share with the Dictyopharidae similar bilaterally symmetrical, usually trilobed, inflatable male genitalia. Emelyanov (1979) transferred some Asian genera from Dictyopharidae to Fulgoridae, citing other characters, but these characters are not diagnostic for New World families.

The stable characters easiest to use are color, especially of the hind wing; the shape

and length of the head process when present; and the shape and carinae of the frons, vertex, and thorax. Since the proportion of the head length to the body length varies greatly with the genera and cannot be determined from the illustrations, measurements are given for the genera (unless it is impossible to get an accurate measurement because of the variability of the curvature of the head process as in *Enchophora*). The ratio of head/pronotum is given for most species. Male genitalia are difficult to inflate consistently, but they are figured for some specimens; I state when I believe they must be used for a valid determination, such as in *Scolopsella*. These descriptions are brief and diagnostic; illustrations are more helpful than words. A character matrix is being prepared and will be published when all of the genera have been studied.

Part I covers those genera with head processes. These keys are artificial. When the definition of genera and placement of species is completed, an attempt will be made to produce cladograms and to identify monophyletic taxa. Two species are consigned to incertae sedis. I do not recognize the genus of *Enchophora ensifera* (Germar) among any New World Fulgoridae or Dictyopharidae, nor *Fulgora caerulescens* Olivier as figured by Stoll (1788, plate 13, Fig. 65) among any New World Fulgoridae or Flatidae.

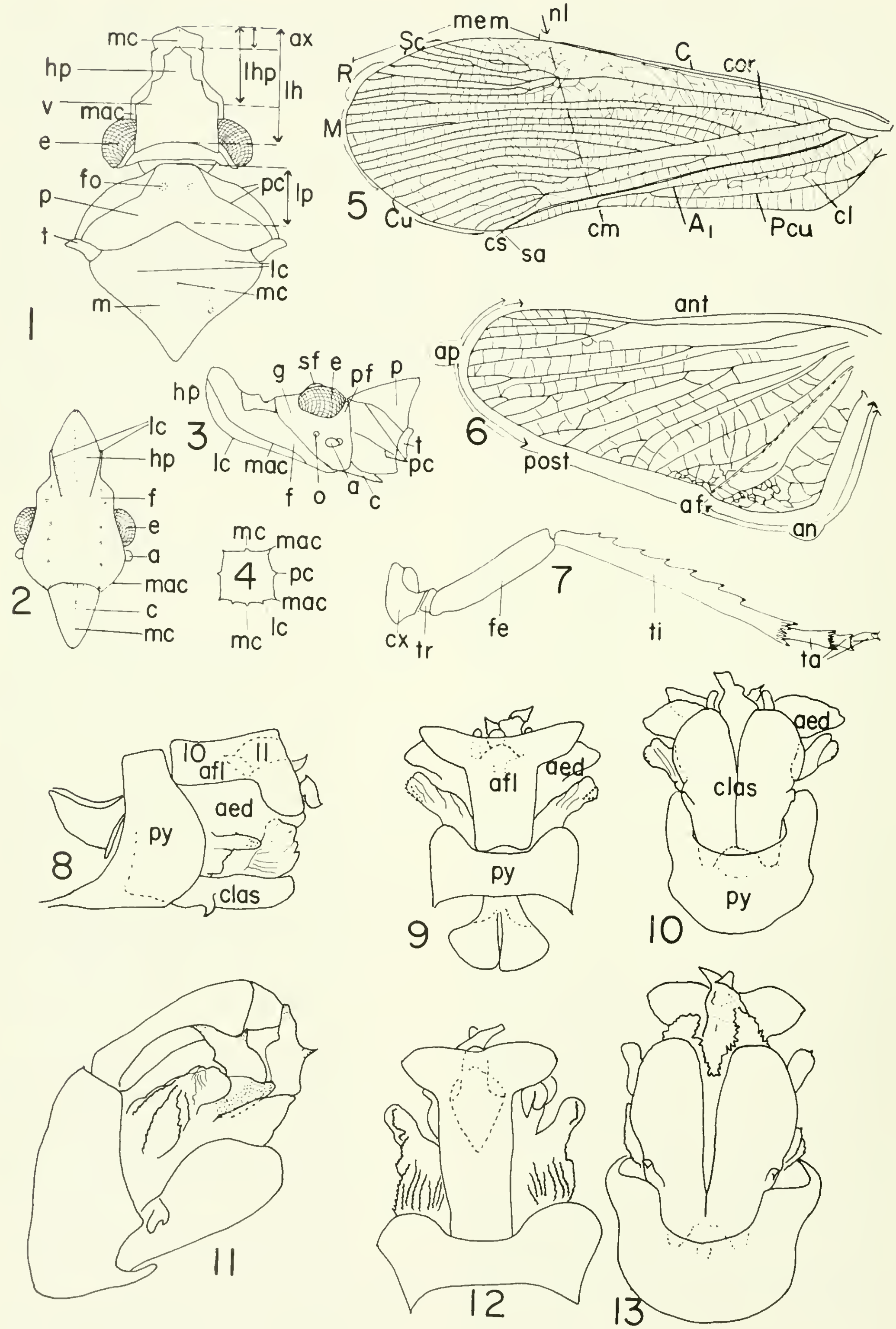
Illustrations of the characters used are found in Figures 1–10 and 33. Three words that may not be commonly used elsewhere are defined as follows: *fossette*—a small, deep pit; *porrect*—extending forward horizontally; *terete*—round in cross section. The head process may have 10 carinae or fewer, which are named in Figure 4. The median vein is pectinate in Figure 5. The convention in Fulgoroidea is to consider the "base" of the insect the dorsal junction between head and thorax, with the base of the head and pronotum both here. The ventral part of the head has its base anterad, at the junction with the vertex, and its apex at the frontoclypeal suture, which is the base of the clypeus.

To save duplication in each section, I have included within the final part of this paper the literature cited for all parts (although papers published subsequent to Metcalf's catalog are cited here); a list of localities with provinces or longitude and latitude (only the city or distance for a city plus elevation where given will be included earlier), and lectotypes or neotypes will be designated. There is a list of genera and species and their distribution by country at the end of this part. Type repository abbreviations are listed in the acknowledgments.

To complete this monograph successfully, I will need help in locating specimens, since many species are known from uniques or one sex only, and distribution records are incredibly incomplete. For at least a year after the publication of this article, I will accept specimens for identification for the traditional recompense, a sample of the specimens in return for identification. Perhaps your specimens will become types. The genus *Chilobia* is a case in point: there are four described species, I have 10 new ones on hand, and only one species is known from more than one specimen. Please help if you have unidentified specimens.

Key to Genera of New World Fulgoridae
with Head Processes

1. Tegmen usually transparent, rarely opaque in basal half . . . . . . . . . . . . . . . . . . . . . . 2
— Tegmen opaque, rarely transparent at apex . . 4
2(1). Tegmen transparent brown with small bristles on veins; prothorax with small, white nodules . . . . . . . . . . . . . . . . . . . . *Enhydria*
— Tegmen without bristles on veins; prothorax without small, white nodules . . . . . . . . . . . . . 3
3(2). Vertex longer than broad (Fig. 1) . . . . . *Stalubra*
— Vertex 3 times as broad as long in midline, emarginate medially (Figs. 51, 54, 60) or apex of vertex hidden by recurved head process (Fig. 57) . . . . . . . . . . . . . . . . . . . . . . . . *Chilobia*
4(1). Each hind wing with an eyespot visible from below with wings unspread; head process gibbous or laterally serrate with narrow apex; large species, over 50 mm in length . . . . . . . . 5
— Hind wings without large, round eyespots; head process porrect or curved, but not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
5(4). Head process peanut-shaped, in lateral view with markings mimicking an alligator head; eyespot on hind wing with iris or pupil . *Fulgora*
— Head process subtriangular, narrowing at apex, strongly serrate (Fig. 26); eyespot on hind wing without iris or pupil . . . . . . *Cathedra*
6(4). Head process porrect (Figs. 14–32, 46–50, 102–117) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
— Head process curved up and back (Figs. 33–35, 40–42, 63–76) . . . . . . . . . . . . . . . . . . . . 7
7(6). Preocular horizontal flange between eye and junction of frons and vertex; head process adpressed to vertex, flattened, rugosely tuberculate (Figs. 33–35) . . . . . . . . . . . . . . . . . *Artacie*




Figs. 1–13. See facing page for identification.

Figs. 1–13. 1–3, 5, 6: *Stalubra brevis* O'Brien: 1, dorsal view, head and thorax; 2, frons and clypeus; 3, lateral view, head; 5, tegmen; 6, hind wing. Hypothetical insect: 4, diagramatic cross section of head process showing position of carinae; 7, stylized hind tibia. Male genitalia, lateral, dorsal, and ventral views: 8–10, *Scolopsella mexicana* O'Brien; 11–13, *Scolopsella reticulata* Ball.

Morphological characters:

a–antenna
$A_1$–1st anal vein
aed–aedeagus
af–anal fold of hind wing
afl–anal flap (10th and 11th abdominal segments)
an–anal area
ant–anterior margin of wing
ap–apical area of hind wing
ax–apex
b–base
C–costa or costal vein
c–clypeus
cl–clavus
clas–clasper
cm–commissural margin
cor–corium
cs–claval suture
CU–cubitus or cubital vein
cx–coxa
e–eye
f–frons
fe–femur
fo–fossette
g–gena
hp–head process
lc–lateral carina
lh–length of head
lhp–length of head process
lp–length of pronotum
M–media, medial vein
m–mesonotum
mac–marginal carina
mc–median carina
mem–membrane of tegmen
nl–nodal line
o–ocellus
p–pronotum
pc–pleural carina
Pcu–postcubital vein
pf–postocular flange
post–posterior area of wing
pr–pronotum
prf–preocular flange (see Fig. 33)
py–pygofer
R–radius, radial vein
sa–sutural angle
Sc–subcostal vein
sf–supraocular flange
t–tegula
ta–tarsomeres
ti–tibia
tr–trochanters
vertex of head

(Continued from page 137)

— Preocular horizontal flange absent; head process usually not adpressed to vertex (see *E. tuberculata*, *subviridis*, *pyrrhocrypta*, Figs. 67, 73, 75) . . . . . . . . 8

8(7). Pronotal median carina raised, with deep fossettes at base; mesonotal apex depressed, striate (Figs. 63–76) . . . . . . . . *Enchophora*

— Pro- and mesonota smooth and gently rounded (Figs. 40–42) . . . . . . . . *Copidocephala*

9(6). Medium-sized species, 26–50 mm in length . . . . . . . . 10

— Small species, under 25 mm in length . . . . . . 13

10(9). Head process with apex twice as wide as narrowest part, dorsolateral edges of process with spines . . . . . . . . *Phrictus*

— Head process with apex not so widened, sides of process without spines . . . . . . . . 11

11(10). Sutural angle of tegmen triangularly produced; head with small, horizontal, preocular flange (Figs. 116–117) . . . . . . . . *Odontoptera*

— Sutural angle of tegmen rounded; head with slight vertical flange on vertical carina (Figs. 27–32) . . . . . . . . 12

12(11). Head process elongate, head 1/3 length of insect, subtriangular, slightly bent dorsad at apex; hind wing clear with veins tinged with green at base, brown elsewhere . . . . *Amerzanna*

— Head process proportionally shorter, less than 1/5 length of insect, with sides subparallel, apex slightly enlarged, not bent dorsad; hind wing brown with either red or white spots . . . . . . . . *Diareusa*

13(9). Head process semicircular in cross section; with dorsal surface slightly compressed, ventral rounded . . . . . . . . *Amycle*

— Head process more nearly rectangular or circular in cross section . . . . . . . . 14

14(13). Head, including process, longer than thorax; tegmen with major veins straight . . . . . . . . 15

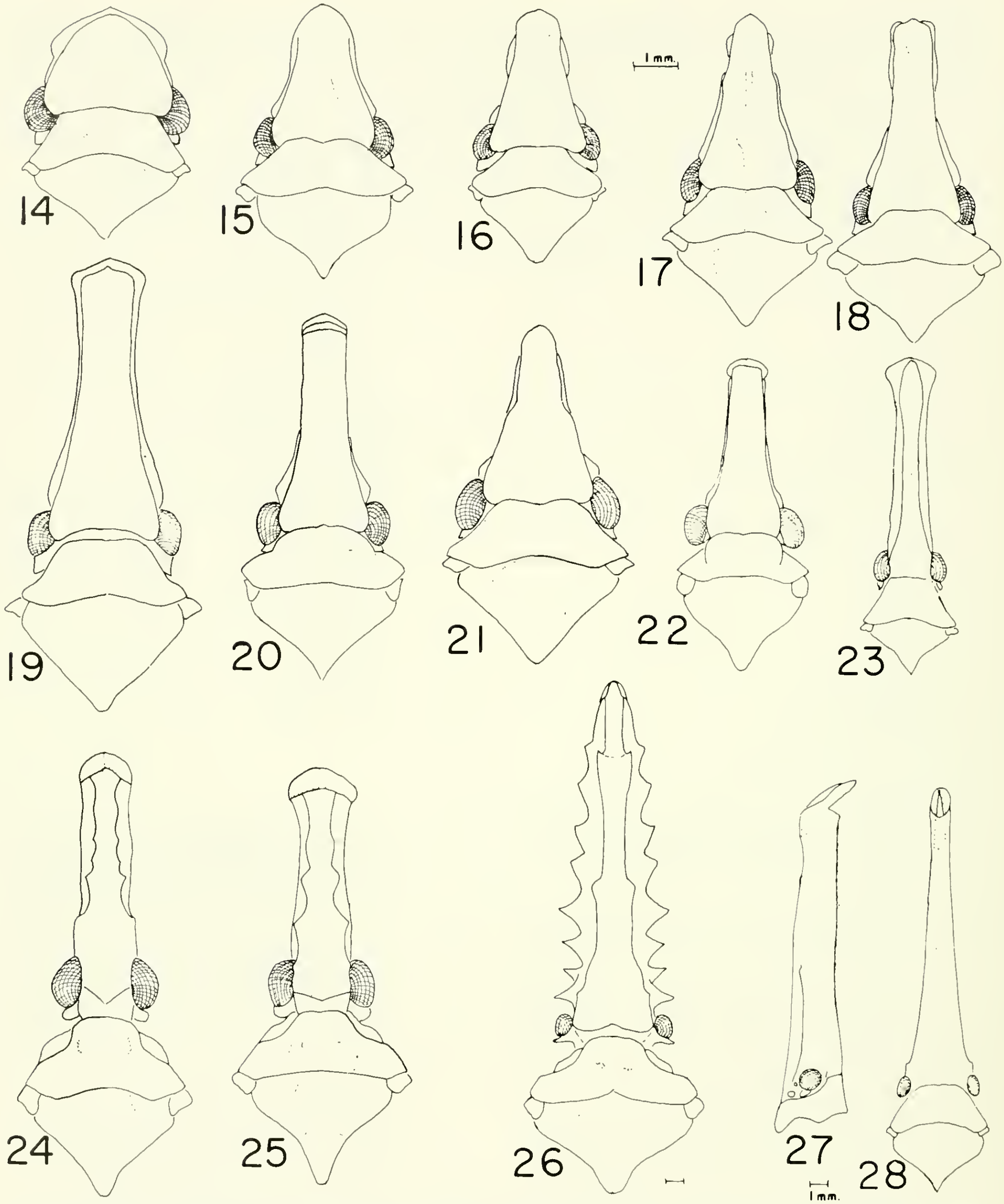
— Head, including process, shorter than thorax; tegmen with major veins irregular, slightly angulate . . . . . . . . 16

15(14). Head process subrectangular in cross section, carinae foliaceous, angulate (Figs. 24, 25) . . . . . . . . *Scolopsella*

— Head process smoothly rounded, almost circular in cross section, carinae normal (Fig. 23) . . . . . . . . *Rhabdocephala*

16(14). Costal margin of tegmen markedly sinuate (Fig. 43); head process not transversely striate . . . . . . . . *Sinuala*

— Costal margin of tegmen slightly convex; head process transversely striate (Fig. 49) . . . . . . . . *Aphrodisias*




Figs. 14–28. Head and thorax, dorsal view: 14, *Amycle brevis* O'Brien; 15, *A. pinyonae* Knull & Knull; 16, *A. saxatilis* Van Duzee; 17, *A. tumacacoriae* Knull & Knull; 18, *A. vernalis* Manee; 19, *A. grandis* O'Brien; 20, *A. sodalis* Stål; 21, *A. mankinsi* O'Brien; 22, *A. amabilis* (Westwood); 23, *Rhabdocephala brunnea* Van Duzee; 24, *Scolopsella mexicana* O'Brien; 25, *S. reticulata* Ball; 26, *Cathedra serrata* (Fabricius); 27, 28, *Amerzanna peruana* O'Brien (27, lateral view).

### *Amerzanna*, n. gen.

Figs. 27, 28

Type-species: *Amerzanna peruana* O'Brien.

Medium-sized, narrow, brown insects, 31–41 mm long, head 1/3 length of insect. Head process porrect, terete, gradually narrowed to apex; apex bent upward; dorsal and ventral median and lateral carinae present on anterior third; weak but traceable pleural carina curving ventrally to end in slight

ventral tubercle. Preocular flange absent. Pronotum smoothly rounded, traces of fossettes and pleural carinae faintly visible. Tegmen with M pectinate; cross-veins irregular, forming diamond-shaped cells. Profemur lonlonger than metafemur, posterior tibia with 6 lateral spines. Ninth abdominal tergite in females twice as long as eighth.

I name this genus *Amerzanna* because superficially it resembles the genus *Zanna* from Africa and Asia. The type-species is *A. peruana*, new species. *Amerzanna* differs from *Odontoptera*, which has the head similarly shaped, by the differences in the tegmina, for it lacks the sharp sutural angle and the spot on the nodal line of *Odontoptera*.

### *Amerzanna peruana*, n. sp.

Figs. 27, 28

LENGTH.—Male 31–33 mm, female 35–41 mm; head 15.6 mm; ratio, head/pronotum 8.3.

Ground color reddish brown. Tegmina well pigmented, transparent, but not obviously so (the hind wings may be seen through the tegmina). Hind wings transparent, greenish cloud at base, brown cloud at apex, brown veins between.

HOLOTYPE (male) and ALLOTYPE (female).—PERU: Madre de Dios: Rio Tambopata Res., 30 air km SW Pto. Maldonada, 290 m, 16–20-XI-1979, J. B. Heppner, subtropical, moist forest (USNM). Paratypes (10 female, 1 male): 3, same data (USNM); 2, 11–15-XI-1979 (USNM); 2 females, 1 male 6–10-XI-1979 (USNM, LOB); 2, Loreto, Ucayali R. Yarina Cocha, 30-XI-1954, leg. Peter Hocking, 1 head process broken (LOB, FMNH); 1, Yahuarmayo, Apc. Group (MCZ).

### *Amycle* Stål

Figs. 14–22, 93–101

*Amycle* Stål 1861:148. Type species: *A. amabilis* (Westwood), subsequent designation by Van Duzee 1916:78

*Cyrpoptus (Amyele) [sic]* Stål, 1862:305.

Small, brown insects, 12–23 mm long, head 1/8 to 1/4 length of insect. Head process porrect, dorsoventrally flattened, dorsal surface flat, ventral convex; usually elongate triangular, but sometimes parallel-sided, sometimes slightly enlarged at apex; dorsal lateral carinae sinuate, it and other carinae variable between species. Preocular flange horizontal, about as produced as marginal carinae. Tegmen with M not pectinate (2 main branches), crossveins reticulate, apical margin more angulate than in most genera. Metatibia with 4–5 lateral spines (sometimes 3 or 7 on a single tibia). Female ninth tergite 1.5–2 times as long as eighth.

This genus may be separated from other small, brown fulgorids by the porrect head being flattened dorsoventrally. It resembles *Cyrpoptus* in wing coloration. Diagnoses are not provided; these species may be identified by the shape of the head (Figs. 14–22) and the color and color pattern of the hind wings (Figs. 93–101).

Key to the Species of *Amycle*

1. Hind wing with 2 colors, brown posterior and base white, yellow, pink, or red (Fig. 93) ..... ........................... *saxatilis* Van Duzee
— Hind wing with 3 colors, brown posterior, translucent area (Figs. 94–101), and base white, yellow, orange, or red ..................... 2
2(1). Base of hind wing yellow, white, or pink ...... 3
— Base of hind wing red or orange .............. 4
3(2). Base of hind wing yellow or yellow-orange, contiguous with brown suffusion, apical area lightly suffused with brown, intermediate area translucent (Fig. 101) ............ *amabilis* (Westwood)
— Base of hind wing pale pink, contiguous with white band, posterior margin brown (Fig. 97); sides of head process parallel (Fig. 18) ....... ............................ *vernalis* Manee
4(2). Vertex at least twice as long as broad (Figs. 17–21) .................................. 5
— Vertex less than twice as long as broad (Figs. 14, 15) ....................................... 8
5(4). Hind wing with brown apical and anal areas contiguous (Figs. 93–97) .................... 6
— Hind wing with transparent area between brown apical and anal areas (Figs. 98–100) ..... 7
6(5). Hind wing with transparent area restricted to narrow anterior band (Fig. 94); head process parallel-sided (Fig. 20) ............. *sodalis* Stål
— Hind wing with transparent area about 1/4 area of wing (Fig. 95); head process subtriangular (Fig. 21) ..................... *mankinsi*, n. sp.
7(5). Head process expanded at tip (Fig. 19); hind wing with red area separated from brown anal and apical areas by transparent band (Fig. 98) ............................. *grandis*, n. sp.
— Head process subtriangular (Fig. 17); red area and brown anal area contiguous (Fig. 100) .... ................... *tumacacoriae* Knull & Knull
8(4). Head broader than long (Fig. 14); apex of hind wing narrowly brown (Fig. 99) ..... *brevis*, n. sp.
— Head longer than broad (Fig. 15); apex of hind

wing broadly brown (Fig. 96) ...............
...................... *pinyonae* Knull & Knull

*Amycle amabilis* (Westwood)
Figs. 22, 101

*Fulgora amabilis* Westwood 1842:119. Type repository: UMO.
*Amycle amabilis* (Westwood), Stål 1861: 148.

LENGTH.—Male 14 mm; head 3.4 mm, ratio, head pronotum 3.1.

Head process elongate, parallel-sided. Hind wing yellow to yellow-orange at base, followed by brown suffusion, apical area less darkly suffused, area between latter two hyaline.

DISTRIBUTION.—Holotype and paratype: MEXICO. No other specimens seen.

*Amycle brevis*, n. sp.
Figs. 14, 99

LENGTH.—Male 13 mm, female 14 mm; head 1.8 mm; ratio, head/pronotum 1.0.

Head triangular, not produced into distinct process (Fig. 14). Hind wing pale orange at base, anal area pale brown, dark brown area on each side of anal fold, apical row of cells brown (Fig. 79). Tegmina in male pale orange with brown maculation apically; in female mottled brown throughout, forming a pattern with a clean, apical, diagonal line.

The two specimens upon which this species is based may represent different species, but the head and hind wings are similar; examination of male genitalia will be necessary to determine whether these are two different species. *A. brevis* may be separated from other species by its short head.

HOLOTYPE (male).—MEXICO: Nayarit, San Blas, 4-IX-1971, W. J. Hansen (LOB). Female (not allotype or paratype): Guerrero: Ciudad Altamirano 20-X-1983, H. Brailovsky, E. Barrera (LOB).

*Amycle grandis*, n. sp.
Figs. 19, 45, 98

LENGTH.—Female 20–22 mm; head 5 mm; ratio, head/pronotum 4.5.

Head elongate, slightly expanded at apex (Fig. 19). Hind wing orange in basal 1/3, brown in anal 1/3 and apical 1/4, translucent areas between (Fig. 98). Tegmina brown with most veins orange-red; two diagonal, brown lines delineating translucent half oval on costa, translucent triangle at apical angle, and mottled brown and white pattern in anal angle (Fig. 45).

HOLOTYPE (female).—MEXICO: Sinaloa, Mazatlan, 5-VIII-1971, D. W. Davis (LOB). Paratype (female): Sonora, Canyon Sapopa, 15-X-1934, Rio Mayo, H. S. Gentry (CIS). Possible male (not paratype): Jalisco, Chapala, 6 mi W Jalisco, 30-VI-1963, J. Doyen (LOB).

*Amycle mankinsi*, n. sp.
Figs. 21, 95

LENGTH.—Female 17 mm; head 3.5 mm; ratio, head/pronotum 2.9.

Head slightly elongate triangular, turned up at apex (Fig. 21). Hind wing red in basal third, apical and anal thirds brown, all colored areas separated from each other by pale areas (Fig. 95). Tegmen brown with most veins red.

I dedicate this species to Dr. J. V. Mankins, with whom we have spent many happy hours collecting.

HOLOTYPE (female).—HONDURAS: Lago Yojoa, 2-IX-1977, J. V. Mankins (LOB). Female paratype: same data except 6-X-1977 (LOB).

*Amycle pinyonae* Knull & Knull
Figs. 15, 96

*Amycle pinyonae* Knull & Knull 1947:397. Type repository: OSU.

LENGTH.—Male 8 mm, female 14–14.5 mm; head 2.6 mm, ratio of head/pronotum 1.9.

Head process triangular, lateral margins sinuate. Hind wing reddish orange in basal 2/5, anal and apical angles brown, translucent area between with brown veins. Tegmen dark brown with many clear areas, these not forming definite pattern.

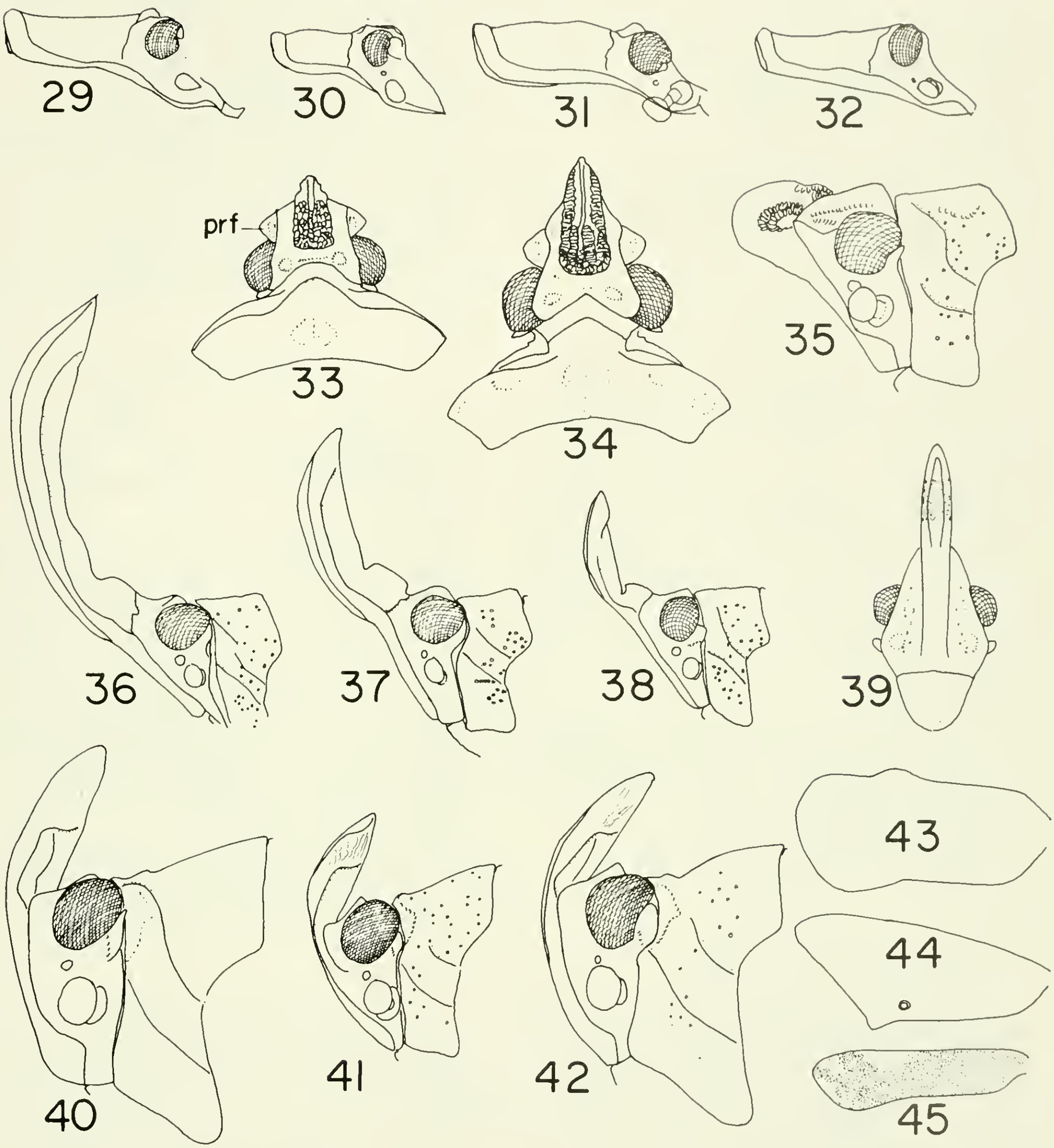
DISTRIBUTION.—Holotype (male): CALIFORNIA: Pinyon Flat, Santa Rosa Mts. on *Pinus cembroides* var. *monophylla* Voss. I have seen three other specimens collected in August from CALIFORNIA: Pinyon Flats and Valvermo and NEW MEXICO: Juan Tabo, 7,000 ft.

*Amycle saxatilis* Van Duzee
Figs. 16, 93

*Amycle saxatilis* Van Duzee 1914:33. Type repository: CAS.

LENGTH.—Male lectotype 12.5 mm; head 2.8 mm, ratio, head/pronotum 3.5.

Head process elongate triangular. Hind wing pale orange at base, followed by white




Figs. 29–45. Head, lateral view: 29, *Diareusa conspersa* Schmidt; 30, *D. kemneri* Ossiannilsson; 31, *D. annularis* (Olivier); 32, *D. imitatrix* Ossiannilsson. Dorsal view: 33, *Artacie haemoptera* (Perty); 34, *A. dufouri* (Signoret). Lateral view; 35, *A. dufouri* (Signoret) (pronotal nodules shown only in lateral view); 36, *Enhydria longicornuta* Lallemand; 37, *E. tessellata* (Walker); 38, *E. cicadina* Gerstaecker. Frontal view: 39, *E. cicadina* Gerstaecker. Lateral view: 40, *Copidocephala merula* Distant (nodules not shown); 41, *C. viridiguttata* Stål; 42, *C. guttata* white. Tegmen: 43, *Sinuala tuberculata* O'Brien; 44, *Odontoptera carrenoi* Signoret; 45, *Amycle grandis* O'Brien.

band, posterior half light brown. Tegmen pale, only slightly darker at apex.

Van Duzee said the color at the base of the hind wing varied from red to luteus in his specimens. This has been verified (N. Penny, personal communication). The color pattern, however, in both specimens has no translucent area.

DISTRIBUTION.—Lectotype, right wing removed and pinned beneath specimen: CALIFORNIA: San Diego County. I have seen no other specimens.

### *Amycle sodalis* Stål
Figs. 20, 94

*Amycle sodalis* Stål 1861:148. Type repository: NRS.

LENGTH.—Male 13–14 mm, female 16.5–18 mm; head 4.5 mm, ratio, head/pronotum 4.5.

Head process elongate, sides parallel to apex. Hind wing orange at base, dark brown posteriorly, anterior 1 1/2 rows of cells behind orange base translucent (Fig. 94). Tegmina red basally, apically translucent with 2 dark apical lines (similar to *Cyrpoptus*); some dark patches caudally.

DISTRIBUTION.—Holotype: MEXICO. I have seen six other specimens collected from July through November from EL SALVADOR: Santa Tecla, 900 m and MEXICO: Atlixco, Canada de Negros, Cordoba, Huachinango.

### *Amycle tumacacorae* Knull & Knull
Figs. 17, 100

*Amycle tumacacorae* Knull & Knull 1947:398. Type repository: OSU.

LENGTH.—Male 14 mm, female 14–15.5 mm; head 3.7 mm; ratio, head/pronotum 3.7.

Head process elongate triangular, slightly widened just before apex, slightly bent dorsad in lateral view. Hind wing red-orange at basal third, dark anal and apical areas, gray membranous areas between with dark veins. Tegmen dark brown with few translucent apical cells. This species is very close to *A. vernalis* in shape and length of head process; it differs in the color and pattern in the hind wing.

DISTRIBUTION.—Holotype (male): ARIZONA: Tumacacori Mts. I have seen 12 other specimens from ARIZONA: Catalina Mts., Chiricahua National Monument, Molino Basin, and Pepper Sauce Canyon; TEXAS: Eastland County, Forestburg, 31 mi W Ozone, Tyler.

### *Amycle vernalis* Manee
Figs. 18, 97

*Amycle[sic] vernalis Manee* 1910:117. Type repository: USNM.

LENGTH.—Female 14.5 mm; head 4 mm; ratio, head/pronotum 4.0.

Head elongate, sides gradually narrowing to apex, apex slightly turned up. Hind wing pale pink in basal fourth, followed by band of white, posteriorly black.

DISTRIBUTION.—Lectotype: NORTH CAROLINA: Southern Pines (USNM). I have seen one other specimen from LOUISIANA: Galbraith.

### *Aphrodisias* Kirkaldy
Figs. 49, 50

*Compsoptera Stål* 1869:236. Type species *C. cacica* Stål, original designation.

*Aphrodisias* Kirkaldy 1906:248, new name for *Compsoptera* Stål.

Small, reddish brown insects, 18–23 mm long, head about 1/8 length of insect. Head process porrect, terete, transversely striate on all sides; dorsolateral carinae present; short, nonstriate, apical portion with dorsal median carina and longitudinal ridge on vertical face. Preocular flange horizontal. Tegmina with longitudinal veins irregularly angled, not straight; few cross-veins. Female ninth tergite slightly longer than eighth.

This genus may be separated from all other genera by the wrinkled, porrect head process. The head process of *Artacie* also is textured, but it is recurved and recumbent on the vertex.

Key to the Species of *Aphrodisias*

1. Head with wrinkled or striate portion of process shorter than pronotum; hind wings red at base, brown apically .................... *cacica* (Stål)

— Head with wrinkled portion of process longer than pronotum; hind wing red, white, and brown ................................ *shaman*, n. sp.

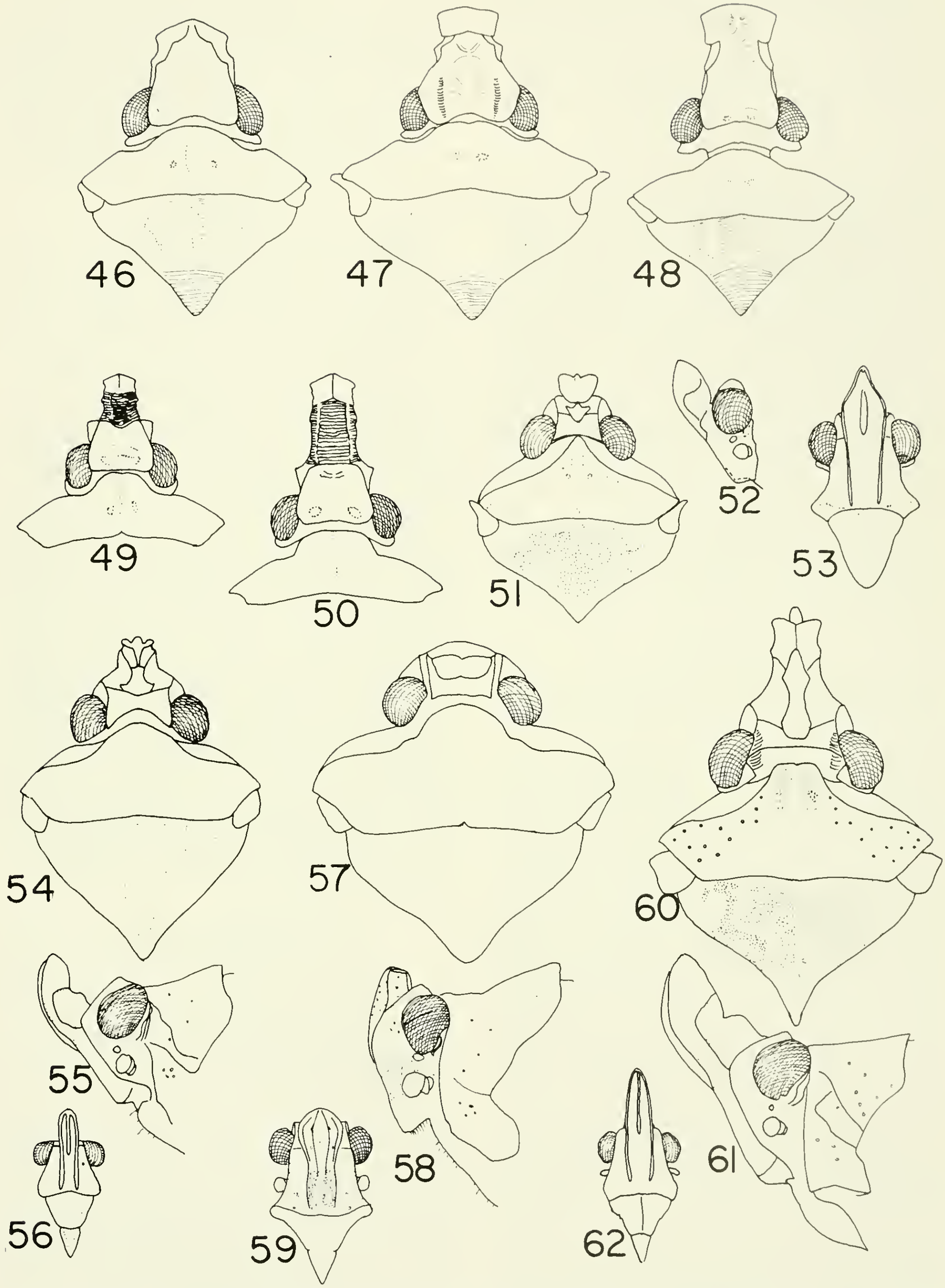
### *Aphrodisias cacica* (Stål)
Fig. 49

*Compsoptera cacica* Stål 1869:237. Type repository: NRS.

*Aphrodisias cacica* (Stål), Kirkaldy 1906:248.

LENGTH.—Male 18–20 mm; head 2 mm; ratio, head/pronotum 1.5.

Head process subequal in length to vertex. Hind wing red at base, brown posteriorly. Tegmen brown.




Figs. 46–62. Head and pronotum, dorsal view: 46, *Sinuala stali* O'Brien; 47, *S. schmidti* O'Brien; 48, *S. tuberculata* O'Brien; 49, *Aphrodisias cacica* (Stål); 50, *A. shaman* O'Brien. Head and thorax, dorsal view and lateral view, and head, ventral view: 51–53, *Chilobia silena* Stål; 54–56, *C. smaragadina* (Walker); 57–59, *C. cinxia* Stål; 60–62, *C. dichopteroides* (Distant).

DISTRIBUTION.—Holotype (female): MEXICO. I have seen six specimens collected from MEXICO: Alamos, 15 mi S Cuernavaca, Cuernonica, from September through November.

*Aphrodisias shaman*, n. sp.
Fig. 50

LENGTH.—Female 23 mm; head 3.5 mm; ratio, head/pronotum 2.3.

Head process 1.7 x longer than vertex. Hind wing pale pink at base, triangular, white area intruding into pink, apex and anal area missing, but edges of anal area brown, apical area brown with white spots.

The wings of this specimen are badly damaged, but it may be separated from *cacica* on the basis of head shape. This specimen has lost its left tegmen and hind wing and part of the right wing, but it is a very distinctive species based on the head alone.

HOLOTYPE (female).—MEXICO: Sinaloa, 5 mi N Mazatlan, 1-VII-1965, J. A. and M. A. Chemsak and E. G. and J. M. Linsley (UCB).

*Artacie* Stål
Figs. 33–35

*Artacie* Stål 1866:132. Type species: *Flata haemoptera* Perty, subsequent designation by da Costa Lima 1935:488.

Brown-winged, medium-sized insects, 20–27 mm long. Head process terete, recurved to lie against vertex (Fig. 35), texture of apex unevenly, rugosely tuberculate, ventral median and marginal carina on process, lateral carinae on frons. Pre- and supraocular flanges large (Figs. 33, 34). Pronotum with white nodules. Tegmina with main veins slightly raised, surface concave between them, M 3-branched, cross-veins reticulate in corium, forming rectangular cells in membrane. Red or orange-red color at base of hind wing almost reaching apical margin medially, dividing it into apical and anal areas.

I synonymized the two species in this genus in 1985. After studying additional specimens, I conclude that I was in error and that the artist's illustrations of the species were correct in each case and there is a difference in the shape of the vertex of the two species. The white spots in the apical portion of the wings do vary in size, placement, and number between specimens, but a general pattern for *haemoptera* is described below.

Key to the Species of *Artacie*

1. Median length of head process before preocular flange subequal to median length of vertex .... ............................ *dufourii* (Signoret)
— Median length of head process before preocular flange half of median length of vertex ......... ............................ *haemoptera* (Perty)

*Artacie dufourii* (Signoret), new status
Figs. 34, 35

*Encophora [sic] dufourii* Signoret 1858:497, pl. 12, no. 2, Fig. 1. Type repository: MZF?
= *Artacie hemoptera* (Perty), O'Brien 1985:661. *Error.*

LENGTH.—Male 25 mm, female 27 mm; head length 2.6 mm; ratio, head/pronotum 1.4. Length of head process in front of preocular flange subequal to length of vertex.

Wings orangish red at base, white spots scattered through brown apical and anal areas, not forming a figure with an empty center (a square, circle, or diamond).

The two known species may be separated by the proportion of the head process in front of the preocular flange to the vertex, subequal in *dufourii* and about half in *haemoptera* (Figs. 33, 34).

DISTRIBUTION.—Type (not seen): CAYENNE. I have seen two other specimens collected in March from FRENCH GUIANA: Maron River; GUYANA: Wineperu. Part of Signoret's collection went to the Naturhistorisches Museum, Vienna, and part to Museo Zoologico dell'Universita degli Studi di Firenze, Florence, according to Horn and Kahle (1935). I did not see the type in Vienna and have not heard from Florence.

*Artacie haemoptera* (Perty)
Fig. 33

*Flata haemoptera* Perty 1833:176, pl. 35, Fig. 3. Type repository: ZSBS, not found.
*Artacie haemoptera* (Perty), Stål 1866:389.
*Encophora [sic] dufourii* Signoret, synonymized O'Brien 1985:661. *Error.*

LENGTH.—Male 20–22 mm, female 23–25 mm; head length 2.1 mm; ratio, head/pronotum 1.2.

Length of head process in front of preocular flange half length of vertex. Wings red at base, brown in apical and anal areas, 4–6 white spots in circle, diamond, or rectangle on apical area, few smaller dots also.

These two species may be separated by the length of the head process and the pattern of white dots on the hind wing.

DISTRIBUTION.—Holotype (not seen) : Amazon basin [BRAZIL?]. I have seen nine other specimens collected in March, August, and October from BRAZIL: Canum, Manaus, Obidos, Rio Negro, and Teffe. The type could not be found in the Zoologische Sammlungen des Bayerischen Staates, Munich, in 1975.

### *Cathedra* Kirkaldy
Fig. 26

*Cathedra* Kirkaldy 1903:179. Type-species: *Phrictus serrata* (F.), original designation.
*Pristiopsis* Schmidt 1905:332. Type-species: *Fulgora serrata* F., original description; synonymized by Distant 1906:20.

Large, yellowish brown insects, 52–71 mm, head 1/3 length of insect. Head process porrect, terete, gradually narrowed to apex; marginal and lateral carinae of frons produced into 11 and 8 spines, respectively; head about 1/3 length of insect. Preocular flange horizontal, spinelike. Tegmen with M irregularly branched (2 main branches); clavus open; cross-veins forming almost round cells anteriorly, arched and parallel behind nodal line. Hind wings brown with ochre eye spot at apex, pale, elongate spots at base, some waxy spots and dashes throughout; emarginate on posterior border before spot.

This monotypic genus has a head process like a cathedral spire, with many pairs of lateral spines, which distinguishes it immediately from any other fulgorid genera.

### *Cathedra serrata* (Fabricius)
Fig. 26

*Fulgora serrata* Fabricius 1781:313.
*Phrictus serratus* (Fabricius), Schaum 1850:65.
*Cathedra serrata* (Fabricius), Distant 1906:20.

LENGTH.—Male 52–53 mm, female 61–71 mm; head 19 mm; ratio head/pronotum 6.3.

Ground color ochre mottled with brown.

DISTRIBUTION.—Holotype: SURINAME. I have studied eight other specimens collected from January to November from BOLIVIA: Santa Cruz; BRAZIL: Manaus-Itacoatiana road, km 30; PANAMA: Barro Colorado Island. Zimsen (1964) did not list the repository of this Fabrician type.

### *Chilobia* Stål
Figs. 51–62

*Chilobia* Stål 1863:237. Type-species: *C. cinxia* Stål, subsequent designation by da Costa Lima 1935:497.
*Ecuadoria* Distant 1906:21. Type-species: *E. dichopteroides* Distant, original designation. *New synonymy.*

Tegmina membranous throughout or membranous in apical half, basal half opaque, brown or brownish red, medium-sized insects, 19–28 mm long. Head process usually recurved, usually dorsoventrally compressed, usually gradually expanding in ventral view towards apex. Lateral carinae of frons parallel or diverging to near base, carinate throughout or becoming broad, fused with median carina into broad hump. Frons elevated above level of frontoclypeal suture, expanded into lobes near apex, with transverse carina extending across frons from lobe to lobe. Vertex with lateral carinae sinuate or angulate in lateral view, supraocular flanges present, apical margin V-shaped, sometimes angulately emarginate medially in addition, sometimes hidden under recurved process. Preocular flange absent. Pronotum with few white nodules. Tegmen with M pectinate (5–8 branches); clavus closed; cross-veins irregular and dense in basal half, few and as thick as longitudinal veins in apical half; longitudinal veins with small spines alternately angled to left or right; transition zone between membrane and opaque area, when present, is arched. Hind wings variable, from only slightly enfumed at base to bright red with sinuate, brown, contiguous area, only two marginal rows of cells enfumed at apex. Female ninth abdominal tergite shorter than eighth.

Because I have intermediates and because the male genitalia are very similar, I have synonymized the genera *Ecuadoria* and *Enhydria* in spite of several character differences. The species of *Ecuadoria* have a long head process and brightly colored tegmen and hind wing, whereas the *Enhydria* species have a short head process, transparent tegmina, and clear hind wings.

The four described species are illustrated, but I have not provided a key because I am unable to determine the range of variation within a species due to lack of available material.

### *Chilobia dichopteroides* (Distant), n. comb.
Figs. 60–62

*Ecuadoria dichopteroides* Distant 1906:22. Type repository: BMNH.

DISTRIBUTION.—Holotype: ECUADOR (NW): Rio Durango, 350 ft. I have seen no other specimens.

*Chilobia cinxia* Stål
Figs. 57–59

*Chilobia cinxia* Stål 1863:238. Type repository: NHMV.

DISTRIBUTION.—Holotype (female): VENEZUELA. I have seen no other specimens.

*Chilobia silena* Stål
Figs. 51–53

*Chilobia silena* Stål 1863:238. Type repository: NRS.

DISTRIBUTION.—Holotype (male): ECUADOR: Quito. I have seen no other specimens.

*Chilobia smaragdina* (Walker)
Figs. 54–56

*Dichoptera smaragdina* Walker 1851:304. Type repository: BMNH.
*Chilobia smaragdina* (Walker), Gerstaecker 1895:39.

DISTRIBUTION.—Holotype: VENEZUELA. I have seen no other specimens.

*Copidocephala* Stål
Figs. 40–42

*Copidocephala Stål* 1869:235. Type-species: *Enchophora guttata* White, original designation.
*Coanaco* Distant 1887:28. Type-species: *Enchophora guttata* White, original designation; synonymized by Distant 1906:23.

Medium-sized, greenish or brown or reddish brown insects, 22–32 mm long. Head process recurved at junction with head, laterally compressed, gradually narrowing anterad; lateral carinae of frons fused at junction with process with medium and lateral carinae of process into one large mound; dorsolateral carina also present on process. Preocular flange absent. Pronotum with small, white, hemispherical tubercles, median carina not strongly humped. Tegmen with M usually pectinate (5–6 branches); corium with crossveins regularly, evenly reticulate, with smooth, sunken, red spots without crossveins; membrane with cells subsquare. Female eighth and ninth abdominal tergites subequal in length.

This genus has the head process curved back at the base, never extending forward as in some *Enchophora;* it is scimitar-shaped like *Enchophora* and *Enhydria*. *Copidocephala* differs from *Enhydria*, which has membranous tegmina, and from *Enchophora* in the characters of the thorax given in that generic discussion. The close proximity of the pronotum and eyes suggests that the postocular flange serves to protect the eye from contact with the pronotum.

Key to the Species of *Copidocephala*

| | | |
|---|---|---|
| 1. | Hind wing black, unspotted ...... | *merula* Distant |
| — | Hind wing brown, spotted with red or blue, green or white ........................... | 2 |
| 2(1). | Large species, 28 mm or longer; hind wing brown with red spots ........... | *guttata* (White) |
| — | Small species, 25 mm or less; hind wing brown with blue, green, or white spots ............ ............................ | *viridiguttata* Stål |

*Copidocephala guttata* (White)
Fig. 42.

*Enchophora guttata* White 1846:331. Type repository: BMNH.
*Copidocephala guttata* (White), Stål 1869:236.

LENGTH.—Female 29–32 mm, head length 1.4 mm; ratio, head/pronotum .63. Pronotum and costal margin of tegmen green, pronotum with red, transverse, sometimes broken, band; ground color of rest of insect ranging from yellow or green through red to olive green. Corium with approximately 21 round, smooth, sunken, small (1 mm or smaller), red spots; spots differing slightly in number, size, and placement among individuals. Hind wing brown with red spots in basal two-thirds.

This species may be separated from *merula*, which is similar in size and coloration, by the absence of red spots in the hind wing in *merula*. It differs from *viridiguttata* in size and in the color of spots in the hind wing, blue or green to white spots in *viridiguttata*.

DISTRIBUTION.—Type: South America. I have seen 20 other female specimens collected from March through September, November and January. PANAMA: Barro Colorado Island, Chiriqui Provence, Fort Clayton; COSTA RICA: 6 mi W Las Canas, La Selva; HONDURAS: Catacamas, 15 km W La Ceiba; MEXICO: Tamazunchale, Temiscal, Volcan Tacana.

*Copidocephala merula* Distant
Fig. 40

*Copidocephala merula* Distant 1906:23. Type repository: BMNH.
*Coanaco melanoptera* Schmidt 1907:361. Type repository: IZW.

*Copidocephala melanoptera* (Schmidt), Metcalf 1947: 176. *New synonymy.*

LENGTH.—Female, 34–38 mm.

Ground color as in *guttata* except hind wing black, without red spots.

The differences in coloration of the tegmen found in the two specimens of *merula* and *melanoptera* are within the variation found in the species *guttata;* so on the basis of size and the color of the hind wing, I synonymize the two species.

DISTRIBUTION.—Holotypes: COLOMBIA (both types). I have seen the type of *merula* but not of *melanoptera*. No other specimens seen.

### *Copidocephala viridiguttata* Stål

Fig. 41

*Copidocephala viridiguttata* Stål 1869:236. Type repository: NHMV.

*Coanaco ornanda* Distant 1887:29, pl. 4, Fig. 13. Type repository: BMNH.

*Copidocephala ornanda* (Distant), da Costa Lima 1935: 491. *New synonymy.*

LENGTH.—Male 22–24 mm; head 1.1 mm; ratio of head/pronotum 0.5.

Ground color olive green with black or red-black, sunken, smooth, round spots in same pattern as *guttata*. Hind wing brown with blue or green to white spots.

This species differs from the other two in having blue, green, or white spots in the hind wing rather than red spots or none. It is interesting that I have 13 males of this species for study and 20 females of guttata. I will examine other collections to see if this is coincidence or unexpected sexual dimorphism. I synonymize *ornanda* on the basis of the shape of the head process and wing coloration.

DISTRIBUTION.—Type: COLOMBIA (*viridiguttata*); syntypes: PANAMA: Bugaba, Tole (*ornanda*). I have studied 13 other specimens collected from May through September and January from PANAMA: Achiote Road, Barro Colorado Island, Fort Clayton; COSTA RICA: Golfito, La Selva; MEXICO: Los Tuxtlas, 3 mi S Palenque.

### *Diareusa* Walker

Figs. 29–32

*Diareusa* Walker 1858:43. Type-species: *Phrictus annularis* (Olivier), by monotypy.

Large, reddish brown insects, 32–49 mm, head relatively short, from .1 to .2 length of the insect. Head process porrect, terete, gradually slightly enlarging at apex; median ventral carina in about anterior third of process, ventral and dorsal lateral carinae complete; short dorsal median carina in anterior portion. Preocular flange vertical, well produced. Tegmen with M sometimes pectinate (3–4 main branches), sometimes evenly branched; cross-veins irregular in corium, forming small squares beyond stigmal line. Tegmen brown throughout with some anterior cells and many spots either white or red; often some apical spots translucent. Female eighth and ninth abdominal tergites subequal in length.

*Diareusa* are large, reddish brown insects with a comparatively short (.1 to .2 length of insect), terete, but not inflated head without transverse striae or spines; these characters will separate them from other New World Fulgoridae. The species differ in the color of spots in the hind wing and in the shape of the head process.

Key to the Species of *Diareusa*

1. Spots on hind wing red and white ........... .......................... *conspersa* Schmidt
— Spots on hind wing white only ............... 2
2(1). Head process short; vertex and head process as long as width of head, including eye ......... ......................... *kemneri* Ossiannilsson
— Head process longer than width of head including eye (Fig. 30) .......................... 3
3(2). Dorsal surface of head process in lateral view convex (Fig. 31) ............. *annularis* (Olivier)
— Dorsal surface of head process in lateral view straight or concave, not convex (Fig. 32) ...... ........................ *imitatrix* Ossiannilsson

### *Diareusa annularis* (Olivier)

Fig. 31

*Fulgora annularis* Olivier 1791:568. Type repository: unknown.

*Phrictus annularis* (Olivier), Walker 1851:264.

*Diareusa annularis* (Olivier), Walker 1858:44.

LENGTH.—Male 32–38 mm, female 45 mm; head 6.2 mm; ratio of head/pronotum 2.2.

Head process in lateral view convex dorsally (Fig. 31.) Hind wings with white spots. These two characters separate it from the other species.

DISTRIBUTION.—Type (not seen): SURINAME. I have seen 10 other specimens collected June to August and January from PERU: Brazilian frontier; BRAZIL: Serra do Navio, Sinop; FRENCH GUIANA: 67 km S Cayenne; SURINAME: Mapane; GUYANA: Shudihat River.

### *Diareusa conspersa* Schmidt

*Diareusa conspersa* Schmidt 1906:375. Type repository: IZW.
*Diareusa dahli* Ossiannilsson 1940:44, Fig. 2. Type repository: UZIL. *New synonymy.*

LENGTH.—Male 38 mm, female 46–49 mm; head 5.3 mm, ratio of head/pronotum 1.8.

Hind wings with red spots. Head process similar to that of *imitatrix*.

This is the most easily identified species in the genus with the spots on the hind wing red and white; in all other species they are white. It is interesting that although this is the easiest character for identification, both Schmidt and Ossiannilsson described this character among the last, causing it to be overlooked. Thus, many museums have *imitatrix*, the common Central American species, identified as *conspersa*. I synonymize *conspersa* and *dahli* on the basis of head shape and wing color.

DISTRIBUTION.—Holotypes: ECUADOR: Palmar (*conspersa*); COLOMBIA: Rio San Agustin (*dahli*). I have seen three other specimens collected from June through August from ECUADOR: Amhuagu, Rio Palenque.

### *Diareusa imitatrix* Ossiannilsson
Fig. 32

*Diareusa imitatrix* Ossiannilsson 1940:45, Fig. 3. Type repository: UZIL.

LENGTH.—Male 35–39 mm, female 43–48; head 5.8 mm; ratio head/pronotum 2.2.

Hind wing with white spots. Head process similar to *conspersa*, but longer and narrower than other species with white-spotted hind wings.

This is the only Central American species and often has been misidentified as *conspersa*. Panamanians call this insect "totoran."

DISTRIBUTION.—Holotype (female): PANAMA: Chiriqui. I have seen 50 other specimens collected all year around from COLOMBIA: Turbo; VENEZUELA: Rancho Grande; PANAMA: Barro Colorado Island, Fortuna, Hartman's Finca, Margarita; COSTA RICA: La Selva, Turrialba; BELIZE: Middlesex; MEXICO: Bonampa R., 1 mi W Fortin de las Flores, Los Tuxtlas.

### *Diareusa kemneri* Ossiannilsson
Fig. 30

*Diareusa kemneri* Ossiannilsson 1940:43, Fig. 1. Type repository: UZIL.

LENGTH.—Male 35 mm; head 4 mm; ratio, head/pronotum 1.8.

Hind wings with white spots. Head process short (Fig. 30). *D. kemneri* may be separated from other white-spotted species by the short head process.

DISTRIBUTION.—Holotype (female): PERU: Perene. I have studied one other specimen collected in September from PERU: Aguaitia.

## *Enchophora* Spinola
Figs. 63–76

*Enchophora Spinola* 1839:221. Type-species: *recurva*, subsequent designation by Duponchel 1840:200.

Medium-sized, reddish brown, green, yellow, or mottled green, white, and red insects, 22–32 mm long. Head process recurved, laterally compressed; nine carinae present on process (all except dorsal median carina). Preocular flange present as vertical carina linking frons and vertex laterally (Fig. 3). Pronotum with pair of deep fossettes laterad of strongly raised median carina. Apex of mesonotum with striate depression between bifurcate median carina. Tegmen with few strong, longitudinal veins, cross-veins variable, dense to average. Female abdominal segments 8 and 9 subequal in length.

*Enchophora* may be separated from the very similar *Copidocephala* by the raised median carina of the pronotum with a fossette or depression on each side, the depression at the apex of the mesonotum surrounded by a high ridge, and the ventrolateral fields of the pronotum being separated from the eye by a space about the width of the last antennal segment. In *Copidocephala* the callus behind the eye almost touches the pronotum when viewed from above, and the pronotum and mesonotum are smoothly rounded. Both genera lack the preocular flange. *Enhydria*, which also has a scimitar-shaped head process, may be differentiated by its pale tegmen and small spines on the tegminal veins.

The species may be separated by the shape of the head process (although this structure varies slightly in curvature and compression), the color of the hind wings, and sometimes by distinctive marks or colors on the body or wings. Waxy spots on the wings may be helpful if they have not been rubbed off; often they may be identified by a smooth, pale brown area if the wax is missing. The hind wings are usually red, yellow, orange, or white in the basal 1/4 to 2/3, measured along the anterior

margin, or 5/6 if measured from anterior to posterior. The color pattern of the tegmen may be quite variable, as in *sanguinea* Distant, *nigromaculata* Distant, and *recurva* (Olivier) where, in females, the tegmen may be concolorous, marked with discrete red or black spots, or marked with coalescent red spots. Although I have not seen both sexes of every species, if there is a sexual difference in color pattern, the male tends to be more evenly mottled and less variable.

Three species listed as *Enchophora* in Metcalf's (1947) catalog have been transferred since to other genera (see list of species).

Key to the Species of *Enchophora*

1. Hind wing with white, waxy points on red area ........................ *stillifera* (Stål)
— Hind wing without white, waxy points on red area .................................. 2
2(1). Head process about twice length of frons before process, enlarged and narrowed near tip (Figs. 63, 64) .......................... 3
— Head process less than twice length of frons before process, scimitar-shaped, curved back over vertex, or curved and then bent upward .......................................... 4
3(2). Apex of head process black, broadly trilobed (Fig. 63) .................. *recurva* (Olivier)
— Head process brown throughout, narrowly expanded at apex (Fig. 64) ..... *tuba* (Germar)
4(2). Hind wing red in basal half; posterior half medium to dark brown; tegmen brown or reddish brown, often mottled ............ 5
— Hind wing white, pale orange, or brown at base; either only apical 1/4 pale brown or posterior half medium brown (*subviridis*, *tuberculata*); tegmen unmottled green or yellow or green mottled with red ............ 9
5(4). Apex of pronotum with transverse, black band (Fig. 66) ........ *nigromaculata* Distant
— Apex of pronotum without transverse, black band .................................. 6
6(5). Mesonotum with black spots (Figs. 67, 76) ... 7
— Mesonotum without black spots ........... 8
7(6). Mesonotum with pair of black spots, also pair on ventrolateral fields of pronotum; head process recurved to near vertex, then bent upward (Fig. 67) ......... *pyrrhocrypta* Walker
— Mesonotum with 2 or 3 pairs of black spots; head process short, only slightly recurved (Fig. 76) .................. *maculata*, n. sp.
8(6). Apical fourth of pronotum pale; base of membrane of tegmen with a brown spot about size of eye on each side, 3–5 other such spots usually present on membrane; ca basal half of hind wing red; abdominal tergites brown .................. *pallidipunctata* Lallemand
— Pronotum concolorous; tegmen not as above; ca basal 2/3 of hind wing red; abdominal tergites bright red ........... *sanguinea* Distant
9(4). Hind wing white at base ................. 10
— Hind wing yellow, orange, or brown at base .......................................... 12
10(9). Tegmen green or yellowish ............. 11
— Tegmen greenish white mottled with red .. .......................... *rosacea* Distant
11(10). Tegmen green or yellowish with white costal margin; head process large (Fig. 71) ....... ....................... *prasina* Gerstaecker
— Tegmen greenish yellow throughout; head process small (Fig. 72) ...... *uniformis*, n. sp.
12(9). Head process scimitar-shaped (Fig. 74); hind wing yellow at base, then white, then brown at apex ................ *viridipennis* Spinola
— Head process recurved and wrinkled (Figs. 73, 75); hind wing orange at base, brown at apex ................................ 13
13(12). Head process recurved, then bent upward at apex (Fig. 75) ............. *subviridis* Distant
— Head process recurved almost to vertex (Fig. 73) .................... *tuberculata* (Olivier)

## *Enchophora maculata*, n. sp.
Fig. 76

LENGTH.—Male 24 mm, female 28 mm.

Ground color brown with minute dots of red and green. Head process short, extending forward then dorsad (Fig. 76). Wings brown on apical third, red basally, red extending from anterior to posterior margin. Distinctive markings: two or three pairs of brown spots on pronotum (Fig. 76); anterior spot black, posterior medium brown, sometimes pale brown spot laterad of latter. Abdominal tergites brownish red.

This species may be identified easily by its unusual, short, partially forward-directed head process (Fig. 76) and the spots on the pronotum.

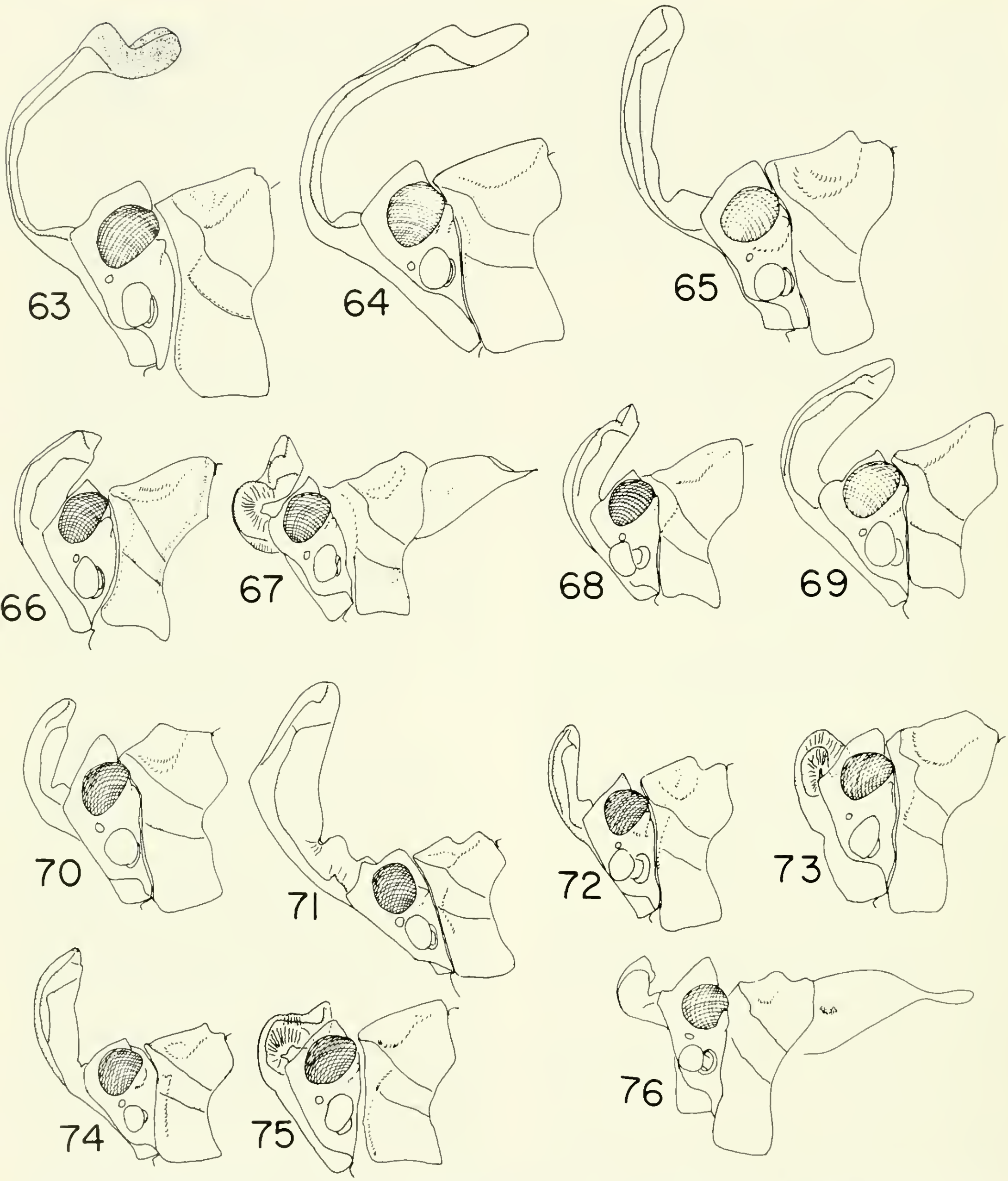
HOLOTYPE (male) AND ALLOTYPE (female).—PERU: Madre de Dios: Rio Tambopata Res., 30 air km SW Pto. Maldonada, 290 m, 16–20-XI-1979, J. B. Heppner, subtropical, moist forest (USNM).

## *Enchophora nigromaculata* Distant
Fig. 66

*Enchophora nigromaculata* Distant 1906:23. Type repository: BMNH.

*E. nigrolimbata* Lallemand 1938:350. Type repository: DEI. *New synonymy.*

LENGTH.—Female 24–26mm.



Figs. 63–76. Head and pronotum, lateral view, of *Enchophora:* 63, *E. recurva* (Olivier); 64, *E. tuba* (Germar); 65, *E. stillifera* (Stal); 66, *E. nigromaculata* Distant; 67, *E. pyrrhocrypta* Walker; 68, *E. pallidipunctata* Lallemand; 69, *E. sanguinea* Distant; 70, *E. rosacea* Distant; 71, *E. prasina* Gerstaecker; 72, *E. uniformis* O'Brien; 73, *E. tuberculata* (Olivier); 74, *E. viridipennis* Spinola; 75, *E. subviridis* Distant; 76, *E. maculata* O'Brien.

Ground color reddish brown, variable, tegmen may be clear, mottled with yellow veins, or with 10 dark spots; membrane brown or with dark spots, 5 to 7 waxy points along nodal line. Head process scimitar-shaped (Fig. 66). Wings red at base, brown posteriorly.

This species may be separated from all other *Enchophora* by the black line along the hind margin of the pronotum. I have not seen the type of *nigrolimbata*.

DISTRIBUTION.—Holotype: BOLIVIA (*nigromaculata*), PERU (*nigrolimbata*). I have seen

11 other specimens collected from October to January from BOLIVIA: Chapare; BRAZIL: Rio de Janeiro; PERU: Chanchamayo; 30 km SW Puerto Maldonado, 290 m; Satipo; Tingo María; Explorama Lodge; ECUADOR: Parque Nacional St. Cecelia.

### *Enchophora pallidipunctata* Lallemand
Fig. 68

*Enchophora pallidipunctata* Lallemand 1966:52. Type repository: FSAG.

LENGTH.—Male 23 mm, female 24–26 mm.

Ground color reddish brown, mottled. Head process scimitar-shaped (Fig. 68). Wings red on basal half, brown posterior half (not the usual 2/3 red, 1/3 brown). Seventeen waxy tufts present in apical area. Distinctive markings: pale band along apical fourth of pronotum and five round, dark spots in tegminal membrane, one on each side just behind nodal line, three to five distad of these. Abdominal tergites brown.

This species may be separated from all other *Enchophora* by the pale apical fourth of the pronotum, the dark spots in the membranous area of each tegmen, and the smaller, red portion of the hind wings. It most closely resembles *sanguinea*, which has the abdominal tergites bright red, while they are brown in *pallidipunctata*.

DISTRIBUTION.—Holotype: BOLIVIA: Buena Vista. I have seen 24 other specimens collected from February through April, August and September from BOLIVIA: Buena Vista, Santa Cruz; PERU: Chanchamayo, Chontilla, Iquitos, Lima, Pileopota, 600 m, Rio Santiago, Satipo, Tarapoto. Several specimens labeled on *Copaifera Dourajeanni* (Leguminosae) at Tingo María, but I am unable to find this species listed in any botanical reference.

### *Enchophora prasina* Gerstaecker
Fig. 71

*Enchophora prasina* Gerstaecker 1895:37. Type repository: EMAU.

LENGTH.—Male 24–27 mm, female, 28 mm.

Ground color green, with costal margin of tegmen white and head and genitalia reddish brown. Head process scimitar-shaped, long, almost as long as mesonotum and pronotum combined. (Fig. 71). Wings white. No waxy tufts evident.

This species may be separated from all other *Enchophora* by the green tegmen with white costal margin.

DISTRIBUTION.—Holotype: COLOMBIA: Nova Granada. I have seen 12 other specimens collected from April through June, and October from BOLIVIA: Buena Vista; PERU: NE; PANAMA: Barro Colorado Island, Cerro Azul, Santa Rita Ridge; COSTA RICA: La Selva.

### *Enchophora pyrrhocrypta* Walker
Fig. 67

*Enchophora pyrrhocrypta* Walker 1851:272. Type repository: BMNH.

LENGTH.—Male 19–20 mm, female 23–25 mm.

Ground color reddish brown, mottled. Head process recurved over pronotum, then bent upward (Fig. 67). Wings red at base, brown posteriorly. Two pairs of distinctive, black spots, one on each side of mesonotum, and one on each ventrolateral margin of pronotum (Fig. 67). No waxy tufts evident.

This species may be separated from all other *Enchophora* by the black marks on the lateral fields of the pronotum and on the sides of the mesonotum (Fig. 67). *E. subviridis* has a similarly recurved head process.

DISTRIBUTION.—Holotype: BRAZIL: Para. I have seen seven other specimens collected from October through February from BRAZIL: Benjamin Constant, Rio Negro, Belem, Mangabeira; GUYANA: Kartabo, St. Laurent; VENEZUELA: Cerro de Neblina.

### *Enchophora recurva* (Olivier)
Fig. 63

*Fulgora recurva* Olivier 1791:34. Type repository: unknown.

*Enchophora recurva* (Olivier), Spinola 1839: 222, pl. 10, Figs. 1, 2

*Enchophora bohemani* Stål 1854:244. Type repository: NRS. *New synonymy.*

LENGTH.—Male 24–26 mm.

Ground color reddish brown, tegmen mottled, often with spots composed of yellow clumped veinlets; membrane with long yellow and brown markings. Head process elongate, produced in club that at apex is twice average width of process, apex trilobed, black (Fig. 63). Wings red at base, brown posteriorly. No waxy tufts evident.

This species may be separated from all other *Enchophora* by the enlarged, blackapex of the head process.

DISTRIBUTION.—Holotypes: BRAZIL (*bohemanni*) and SURINAME (*recurva*). I have seen nine other specimens from BRAZIL: Linhares, Araxa, and Painaivas, taken from October through December. I am unable to confirm Berg's report from Argentina (Berg 1879).

### *Enchophora rosacea* Distant
Fig. 70

*Enchophora rosacea* Distant 1887:27, pl. 4, Fig. 11. Type repository: BMNH.

LENGTH.—Male 22–23 mm, female 25–26 mm.

Ground color green, tegmen at base greenish white with distinctive clumps of red dots between the green veins; membrane green with 20 white, waxy spots. Head process scimitar-shaped (Fig. 70). Wings mostly white, dusted with red spots at base, brown posteriorly.

This species may be separated from all other *Enchophora* by the red and green combination on the tegmen.

DISTRIBUTION.—Holotype: NICARAGUA: Chontales. I have seen 10 other specimens collected from March through August from PANAMA: Barro Colorado Island; COSTA RICA: La Selva.

### *Enchophora sanguinea* Distant
Fig. 69

*Enchophora sanguinea* Distant 1887:27, pl. 4, Fig. 16. Type repository: BMNH.
*Enchophora florens* Distant 1887:28, pl 4, Fig. 12. Type repository: BMNH. *New synonymy*.
*Enchophora longirostris* Distant 1887:28. Type repository: BMNH. *New synonymy*.

LENGTH.—Male 22–23, female 24–25 mm.

Ground color greenish to reddish, tegmen greenish or reddish, or greenish black with orange or red spots encircled with yellow veins, or the red spots may be fused into large areas or confluences, usually very mottled with clumps of yellow veins and dark and/or light spots. Head process scimitar-shaped (Fig. 69). Wings red at base, brown posteriorly. Twenty waxy tufts present in membranous area of tegmen. Abdominal tergites bright red.

I synonymize this species with two other species; *E. florens* and *longirostris* have the same male genitalia; *E. sanguinea* differs from them only in the pattern of the tegmen. When I found comparable difference in coloration in other species, I felt confident in synonymizing the three. This species may be separated from all other *Enchophora* with red hind wings by the shape of the head and the lack of distinctive identifying marks such as bands and spots on the pronotum.

DISTRIBUTION.—Type: GUATEMALA, PANAMA (*sanguinea*). NICARAGUA: Chontales (*florens*); COSTA RICA: Cache. COLOMBIA (longirostris). I have seen 39 other specimens collected from July to September, with one in February. ECUADOR: Palmar; PANAMA: Barro Colorado Island, Cana 1,200 ft; COSTA RICA: 1 mi N Tucurrique, Rincon, Turrialba, Cairo.

### *Enchophora stillifera* (Stål)
Fig. 65

*Phrictus stillifera* Stål 1862:303. Type repository: NHMV.
*Enchophora stillifera* (Stål), Stål 1864:49.

LENGTH.—Male 25–28 mm, female 32 mm.

Ground color greenish brown, tegmen often with spots of clumped yellow veins, also often with broad patches of waxy exudate. Head process elongate, scimitar-shaped, about twice as long as frons below process. Wings red at base, mottled with white, waxy spots; brown posteriorly.

This distinctive species is the only *Enchophora* with many white, waxy spots on the red portion of the hind wing.

DISTRIBUTION.—Holotype (male): MEXICO; GUATEMALA: Sabo; PANAMA: Bugaba, 2,000–3,000 ft. I have seen 24 other specimens collected from June to October from PANAMA: Chiriqui, Lino; COSTA RICA: Osa Peninsula; HONDURAS: Orina del Rio Camgre, Juticalpa; BELIZE: Northern Road, mi 28–45; MEXICO: San Quintin.

### *Enchophora subviridis* Distant
Fig. 75

*Enchophora subviridis* Distant 1887:28, pl. 4, Fig. 17. Type repository: BMNH.
*Enchophora subviridis* var. *a*. Distant 1887:497.
*Enchophora subviridis distanti* Metcalf 1938:358.

LENGTH.—Male 22 mm, female 23–25 mm.

Ground color green, brown, or yellow. Head process reflexed, then turned up at tip. Wings orange in basal half, brown posteriorly; 8 waxy tufts in costal margin of tegmen, 20 plus in membrane.

This species may be separated from all other species but *pyrrhocrypta* by the recurved and bent dorsad head process, and

*pyrrhocrypta* has distinctive, black spots on the pro- and mesonota and red on the hind wings.

DISTRIBUTION.—Syntypes: PANAMA: Chiriqui, Bugaba. I have seen six other specimens collected from August to October from PANAMA: Chiriqui, Bugaba, 800–1,500 ft; COSTA RICA: Puntarenas Prov., Osa Peninsula, Rincon; San Vito, Golfito.

### *Enchophora tuba* (Germar)

Fig. 64

*Fulgora tuba* Germar 1830:46. Type repository: Lvov. (All types there are lost.)
*Enchophora tuba* (Germar), Burmeister 1845:4.

LENGTH.—Female 30 mm.

Ground color reddish brown, mottled. Head process elongate, produced in club that at apex is twice average width of process, apex trilobed, brown like rest of process (Fig. 64). Wings red at base, brown posteriorly. No waxy tufts evident.

This species may be separated from all other *Enchophora* by the long, thin head process with a trilobed, concolorous tip.

DISTRIBUTION.—Type: BRAZIL. I have seen two other specimens collected from BRAZIL: Agua Preta, in December.

### *Enchophora tuberculata* (Olivier)

Fig. 73

*Fulgora tuberculata* Olivier 1791: 569. Type repository: unknown.
*Enchophora tuberculata* (Olivier), Burmeister 1845: [4].
*Enchophora tuberculata* sub. sp. *fuscomaculata* Lallemand 1956:6. Type repository: FSAG.
*Enchophora parvipennis* Walker 1858:30. Type repository: BMNH. *New synonymy*.

LENGTH.—Male 22 mm.

Ground color greenish brown. Head process recurved toward vertex (Fig. 73). Wings brown, orange in anterior four cells. No waxy tufts evident.

This species may be separated from all other *Enchophora* by the recurved head process, which differs from *pyrrhocrypta* and *subviridis* by not being turned up at the tip. The basal colored area of the hind wing is also more reduced than in any other species; in one specimen it is brown with the four cells slightly paler brown.

DISTRIBUTION.—Type: SURINAME (*tuberculata*); BRAZIL: Para (*parvipennis* male). I have seen two other specimens from FRENCH GUIANA: St. Jean du Moroni; VENEZUELA: Salto de las Acadencias.

### *Enchophora uniformis*, n. sp.

Fig. 72

LENGTH.—Male 24–26 mm, female 25–26 mm.

Ground color yellow to greenish yellow. Head process scimitar-shaped, shorter than frons below process. Hind wing white with apical third yellowish. Tegmen with margin darker behind stigmal line; this margin with eight spots that may be indicators of waxy tufts. Distinctive markings, brown or black: apex of supraocular flange, three or more dashes along clavus, spots along stigmal line (these are variable; one specimen lacks them all).

This species has a smaller process than *viridipennis* and *prasina*, the only two other species with green or yellow tegmen. It lacks the white costal margin of *prasina* and the yellow-orange base of the hind wing of *viridipennis*.

DISTRIBUTION.—Holotype (male), allotype (female), and 1 paratype (female): PERU: Iquitos, F6062, H. Bassler Colln. Acc. 33591 (AMNH). Four other paratypes: PERU: Chauchamayo [*sic*], from W. F. H. Rosenberg (NCU, male); Jauja Prov. Satipo, Sept. 1946, A. Maller Coll., Frank Johnson Donor (AMNH, female).; Dept. Huanuco, Vic. Tingo María, Jungle, 670 m, XII-1939, Felix Woytkowski (AMNH, male); Iquitos, Rio Itaya, Herbert Osborn Colln (OSU, female).

### *Enchophora viridipennis* Spinola

Fig. 74

*Enchophora viridipennis* Spinola 1839:225, pl. 11, Fig. 2. Type repository: NHMV.
*Enchophora eminenta* Schmidt 1909:187. Type repository: IZW. *New synonymy*.

LENGTH.—Male 22 mm.

Ground color yellow brown (given as green in original description). Head process scimitar-shaped, shorter than most other species (Fig. 74). Hind wings yellow-orange at base, posteriorly white with ochre veins. More than 10 waxy tufts present along slightly infuscate margin of tegmen.

This species may be separated from all other *Enchophora* but *uniformis* by the coloration of the hind wings. In the specimen examined the distinctive color markings are

the shiny, black apex of the head process, a black spot on each side of the frons before the eye, five very small, red marks on the tegmen, red longitudinal lines on the clypeus, a diagonal, red, marginal band on each side of the pronotum, and the browner wing margin. Schmidt (1909) described the clypeus as having blood-red longitudinal stripes, the apex of the clypeus, the pronotum and scutellum, the legs, and the five spots on the tegmen blood red. The specimen at hand has fainter coloration. Spinola (1839) said that the spots on the tegmen are black. I did not have a specimen to compare with either of these types when I visited their respective museums; so, I am placing them in synonymy by utilizing their descriptions and illustrations and my notes.

DISTRIBUTION.—Holotype: BRAZIL: Pebas (*eminenta*), locality unknown (*viridipennis*). I have seen one specimen from BRAZIL: Jacareacanga, collected in February.

## *Enhydria* Walker
Figs. 36–39

*Enhydria* Walker 1858:44. Type-species: *Dichoptera tesellata* Walker, by monotypy.
*Ulubra* Stål 1866:133. Type-species: *U. brachialis* Stål, by monotypy. Synonymized by Stål 1870:286. *Ulubra* resurrected by O'Brien 1985:662. [Error] *New synonymy*.

Medium-sized, brown insects with transparent tegmina, 19–22 mm long. Head process recurved, laterally compressed, gradually narrowing to apex. All five ventral carina and two dorsolateral carina present, complete; dorsal median carina present at base of process, extending as far as dorsal notch. Preocular flange horizontal, small. Pronotum with white nodules. Tegmen with short spines along veins on upper surface, M not pectinate; cross-veins along costal margin dense, diagonal; other cross-veins not dense, about same diameter as longitudinal veins; most cells rectangular. Female with eighth and ninth abdominal tergites subequal.

This genus may be separated by the short spines on the veins on the upper surface of the tegmen and the transparent, brown hind wing. The dorsal head measurement and head/pronotal ratio were not made in this genus because the length varies greatly with the position of the head process.

I resurrected *Ulubra* as a valid genus on the basis of illustrations and notes taken from a specimen so identified at the British Museum. Recently, I discovered a photograph of the type of *Ulubra brachialis* taken in Stockholm; and it is a synonym of *tessellata*. The genus I resurrected as *Ulubra* is renamed below as *Stalubra* (*q. v.*).

All species of *Enhydria* have a similar color pattern: brown insects with red spots on the pronotum, black markings on the head process, etc. They may be identified to species by the length and shape of the head process.

Key to the Species of *Enhydria*

1. Head in lateral view with distance from frontoclypeal suture to dorsal notch greater than length from dorsal notch to apex, thus process short (Figs. 37, 38) .......................... 2
— Head in lateral view with distance from frontoclypeal suture to dorsal notch on process less than length from dorsal notch to apex, thus process long (Fig. 36) ...... *longicornuta* Lallemand

2(1). Venter of process black; thickness of process in lateral view about 1/2 width of eye (Fig. 38) ... .......................... *cicadina* Gerstaecker
— Venter of process pale with brown spots, only tip black; thickness of process in lateral view subequal to width of eye (Fig. 37) ............... ............................ *tessellata* (Walker)

## *Enhydria cicadina* Gerstaecker
Figs. 38, 39

*Enhydria cicadina* Gerstaecker 1895:38. Type repository: EMAU.

LENGTH.—Male 19.5–21.5 mm.

This species has the shortest head process (Fig. 38).

MALE GENITALIA.—The two pairs of inflatable lobes have darkened, tuberculate tips, which the other species do not have.

DISTRIBUTION.—Syntypes: BRAZIL: Bahia. I have seen six other specimens collected in December from BRAZIL: Caviuna, Iguazu Falls, and Tijuco Preto.

## *Enhydria longicornuta* Lallemand
Fig. 36

*Enhydria brachialis* f. *longicornuta* Lallemand 1960:106. Type repository: NRS.
*Enhydria longicornuta* Lallemand, O'Brien 1985:661.

LENGTH.—Male 20–22 mm, female 20–22 mm.

This species has the longest head process (Fig. 36).

MALE GENITALIA.—The ventral lobe in ventral view has a slight median projection and is

about half as wide as the claspers.

DISTRIBUTION.—Holotype: BRAZIL. I have seen five other specimens collected from BRAZIL: Manaus, Serro do Navio, and TRINIDAD.

*Enhydria tessellata* (Walker)
Fig. 37

*Dichoptera tessellata* Walker 1851:305. Type repository: BMNH.
*Enhydria tessellata* (Walker), Walker 1858:44.
*Enchophora brachialis* Stål 1862:1. Type repository: NRS. *New synonymy.*
*Enhydria brachialis* (Stal), da Costa Lima 1935:497.

LENGTH.—Male 19–20 mm, female 21–22 mm.

This species has a medium-length head process (Fig. 37).

MALE GENITALIA.—Ventral lobe of the aedeagus with median emargination, ventral lobe about as wide as claspers.

DISTRIBUTION.—Holotype: BRAZIL: Rio de Janeiro (*brachialis* male); Para (*tessellata* female). I have seen 11 other specimens collected in January, March, June, and October from BRAZIL: Corcovado, Faz Morelandia, Corupa, and Para; PERU: Tingo María.

*Fulgora* Linnaeus
Figs. 77–92

*Fulgora* Linnaeus 1767:703. Type-species: *F. laternaria* (Linnaeus), subsequent designation by International Commission on Zoological Nomenclature, Opinion 322 (1954:187).

Large insects, 65–105 mm in length, yellowish brown mottled with black markings and white, waxy areas, head .25 to .28 length of insect. Head process porrect, terete, inflated, resembling a peanut from above and an alligator head, including false eye spots, in lateral view. Preocular flange large, horizontal. Tegmen with M not pectinate, most crossveins forming many-sided, almost round cells. Female with abdominal tergites eight and nine subequal in length.

At the museum in Sao Paulo, I examined the specimens used by da Fonseca (1926) in his revision; these did not fit his key. B. V. Ridout (personal communication) examined previously used characters and several new features, including male genitalia and the results of morphometric analyses, and found the best way to identify species in this genus was to match specimens to the accompanying illustrations of head shapes. His illustrations are labeled lectotype except for *lampetis* (holotype), *crocodilia*, and *lucifera*. I give him full credit for this section and am convinced that this is the best that can be done at this time. Any errors are mine.

Ridout suggested that species with narrow heads might live in dry forests, the others in rain forests. Janzen (1983) described the behavior of *F. laternaria*, including at least 100 specimens seen resting on *Hymenaea courbaril* or guapinol, but questioned whether this plant is the host or only host, as it does not extend throughout the range of the insect species.

*Fulgora castresii* Guerin-Meneville
Figs. 81, 82

*Fulgora castresii* Guerin-Meneville 1837:3, pls. 173, 174, Figs. 3, 4.

DISTRIBUTION.—Type: MEXICO. I have seen 10 specimens collected from July through September from MEXICO: Hustusco, Nuevo X-Can [*sic*], Tamazunchale; PERU: Tingo María: PANAMA: Barro Colorado Island.

*Fulgora cearensis* Forseca
Figs. 87, 88

*Laternaria cearensis* Fonseca 1932:3, Figs. 1, 2, 3h.
*Fulgora cearensis* Fonseca, Metcalf 1947:219.

DISTRIBUTION.—Type: BRAZIL. I have seen two specimens from TRINIDAD: Curepe and Maraval, collected in September.

*Fulgora crocodilia*
Brailovsky & Beutelspacher
Figs. 85, 86

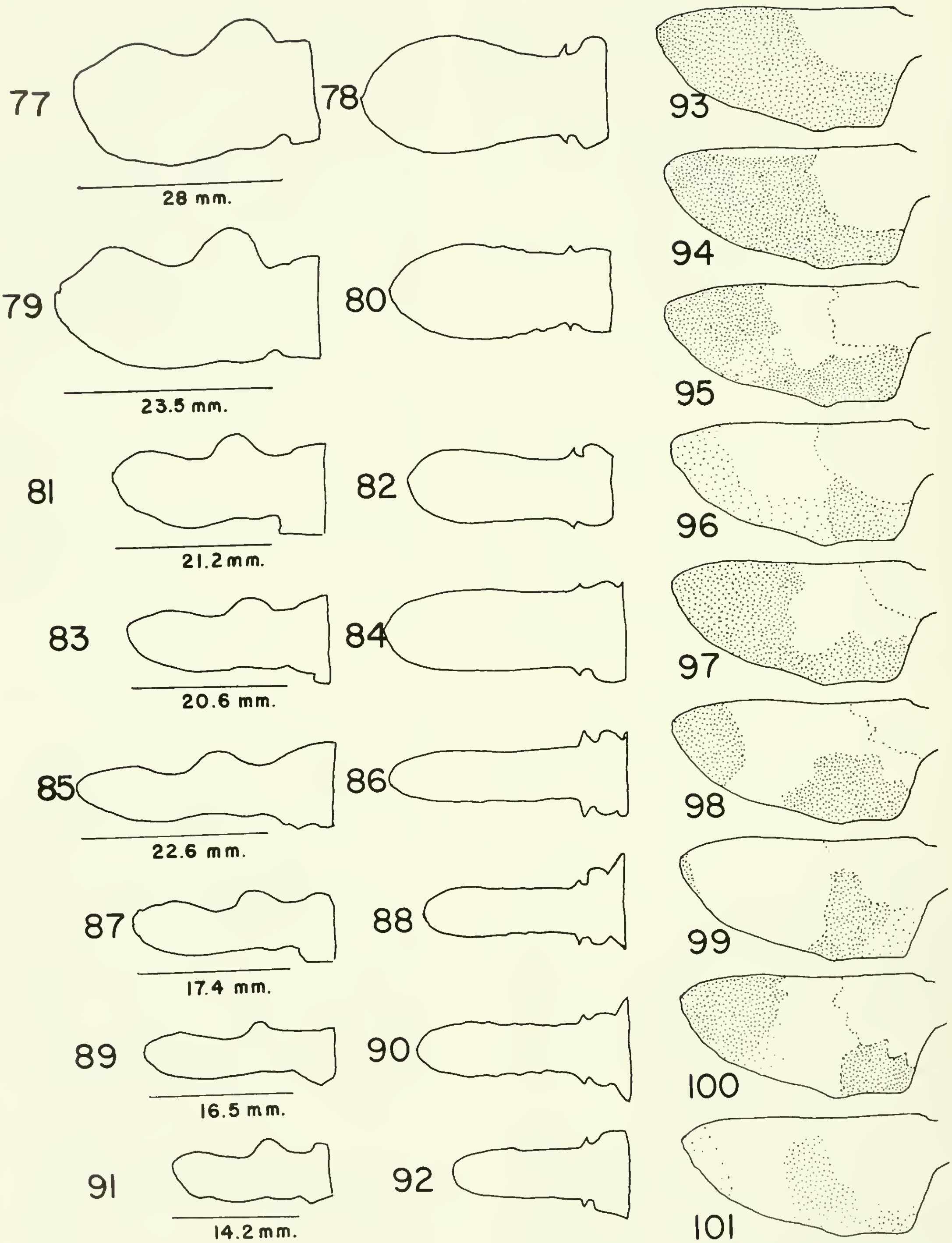
*Fulgora crocodilia* Brailovsky & Beutelspacher 1978:176, pl. 3.

DISTRIBUTION.—Type: MEXICO. I have seen three specimens collected from MEXICO: Chamela, in September and November.

*Fulgora graciliceps* Blanchard
Figs. 83, 84

*Fulgora graciliceps* Blanchard 1849:pl. 2, Fig. 1.
*Laternaria orthocephala* Fonseca 1926:493, pl. 6, Figs. 1, 2. *New synonymy*, Ridout.
*Fulgora orthocephala* Fonseca, da Costa Lima 1942:42.

DISTRIBUTION.—Type: BRAZIL (*orthocephala, graciliceps* unknown). I have seen three specimens from BOLIVIA: Requena and Warnes, and PERU: Tingo María, collected in November.




Figs. 77–101. Head, dorsal view (odd numbers), lateral view (even numbers): 77–78, *Fulgora lampetis* Burmeister; 79–80, *F. laternaria* (L.); 81–82, *F. castresii* Guerin-Meneville; 83–84, *F. graciliceps* Blanchard; 85–86, *F. crocodilia* Brailovsky & Beutelspacher; 87–88, *F. cearensis* Fonseca; 89–90, *F. lucifera* Germar; 91–92, *F. riograndensis* Fonseca. Hind wings of *Amycle*: 93, *A. saxatilis* Van Duzee; 94, *A. sodalis* Stål; 95, *A. mankinsi* O'Brien; 96, *A. pinyonae* K & K; 97, *A. vernalis* Manee; 98, *A. grandis* O'Brien; 99, *A. brevis* O'Brien; 100, *A. tumacacoriae* K & K; 101, *A. amabilis* (Westwood).

### *Fulgora lampetis* Burmeister
Figs. 77, 78

*Fulgora lampetis* Burmeister 1845:3.

DISTRIBUTION.—Type: BRAZIL. I have seen 11 specimens collected throughout the year from BOLIVIA: La Cordillera Santa Cruz; PERU: Tingo María; BRAZIL: Obidos, Sinop; PANAMA: Barro Colorado Island; COSTA RICA: Sarapiqui; NICARAGUA: Leon; HONDURAS: La Ceiba.

### *Fulgora laternaria* (Linnaeus)
Figs. 79, 80

*Cicada laternaria* Linnaeus 1758:434.
*Fulgora laternaria* Linnaeus, Linnaeus 1767:703.
*Fulgora servillei* Spinola 1839:214. *New synonymy*, Ridout.

DISTRIBUTION.—Type: Tropical America (*laternaria*); BRAZIL (*servillei*). I have seen five specimens collected in January, and April through July in PANAMA: Barro Colorado Island; HONDURAS: Armenta, La Ceiba; MEXICO: Los Tuxtlas.

### *Fulgora lucifera* Germar
Figs. 89, 90

*Fulgora lucifera* Germar 1821:100.
*Fulgora mitrii* Burmeister 1867:xxiii, Berg 1879:178.

DISTRIBUTION.—Type: BRAZIL. I have seen 16 specimens collected from November through February from ARGENTINA: Abra Grande Iran; BOLIVIA: Coipa, El Torno, Mora Abado Iz., Montero, Santa Cruz, and Warnes.

### *Fulgora riograndensis* Fonseca
Figs. 91, 92

*Laternaria servillei riograndensis* Fonseca 1926:486, pl. IV, Fig. 1.
*Laternaria riograndensis* Monte 1932:22.
*Fulgora riograndensis* Fonseca, Metcalf 1947:232.

DISTRIBUTION.—Type: BRAZIL. I have seen one specimen from PANAMA: Barro Colorado Island, collected in June.

### *Odontoptera* Carreno
Figs. 44, 116, 117

*Odontoptera* *Carreno* 1841:275. Type species: *O. spectabilis* Carreno, by monotypy.

Medium-sized, green or brown insects, 27–37 mm long, head 1/6 to 1/3 length of insect. Head process porrect, terete, elongate triangular; apex bent dorsad; lateral carinae of dorsum and venter and pleural carinae all visible. Preocular flange small, diagonal or horizontal. Ventropleural carina of pronotum present, dorsopleural carina absent, represented by low ridge. Tegmen with apex truncate; anal angle angulate; dark spot along stigmal line; M greatly expanded, 16–19 branches at level of stigmal line; cross-veins incomplete in corium, forming rectangular cells in membrane. Female with eighth and ninth abdominal tergites subequal in length.

*Cathedra serrata* and the two species of this genus are the only Fulgoridae with head processes which I have never seen misidentified.

Key to the Species of *Odontoptera*

1. Head about 1.5 times as long as pro- and mesonota combined; tegmen green with narrow, apical, brown band; hind wing green with brown and orange markings .... *carrenoi* Signoret

— Head almost as long as pro- and mesonota combined; tegmen orange-brown basally, brown behind pale, thin, nodal band; hind wing white at base, brown apicallly ........ *spectabilis* Carreno

### *Odontoptera carrenoi* Signoret
Figs. 44, 117

*Odontoptera carrenoi* Signoret 1849:178, pl. 6, Fig. 4. Type repository: NHMV.

LENGTH.—Male 27–28 mm, female 30–33 mm; head length 9.7 mm; ratio, head/pronotum 5.4.

Ground color green with brown apical band on tegmen, round, black spot surrounded by white line at apex of clavus on stigmal line (Fig. 44). Hind wing green with two black spots near anal angle, spots surrounded by orange area.

This species is green with a more elongate head than the brown *spectabilis*.

DISTRIBUTION.—Holotype: locality unknown. I have seen 26 other specimens, collected May to October and February, from: BRAZIL: Sinop; FRENCH GUIANA: Montagne des Singes near Kourou; 67 km S Cayenne; PANAMA: Barro Colorado Island, Santa Rita Arriba, Parque Nacional Soberania Frijolito; COSTA RICA: La Selva; MEXICO: Los Tuxtlas.

### *Odontoptera spectabilis* Carreno
Fig. 116

*Odontoptera spectabilis* Carreno 1841:277, pl. 5, Fig. 2. Type repository: ZMHB.

LENGTH.—Female 36–37 mm; head length 5.8 mm; ratio, head/pronotum 2.3.

Ground color yellow-orange on head, thorax, and apical part of tegmina, tegmen behind stigmal line brown. Head, thorax, and tegmen with lateral, longitudinal, brown band extending half length of costa. Hind wing white, black along apical margins, tinged with orange at base.

This species is brown and has a shorter head than the green *carrenoi*.

DISTRIBUTION.—Type: America (?). I have seen four other specimens, collected from January to March, from BRAZIL: Boraceia Field Station and Corupa.

### *Phrictus* Spinola
Figs. 102–115

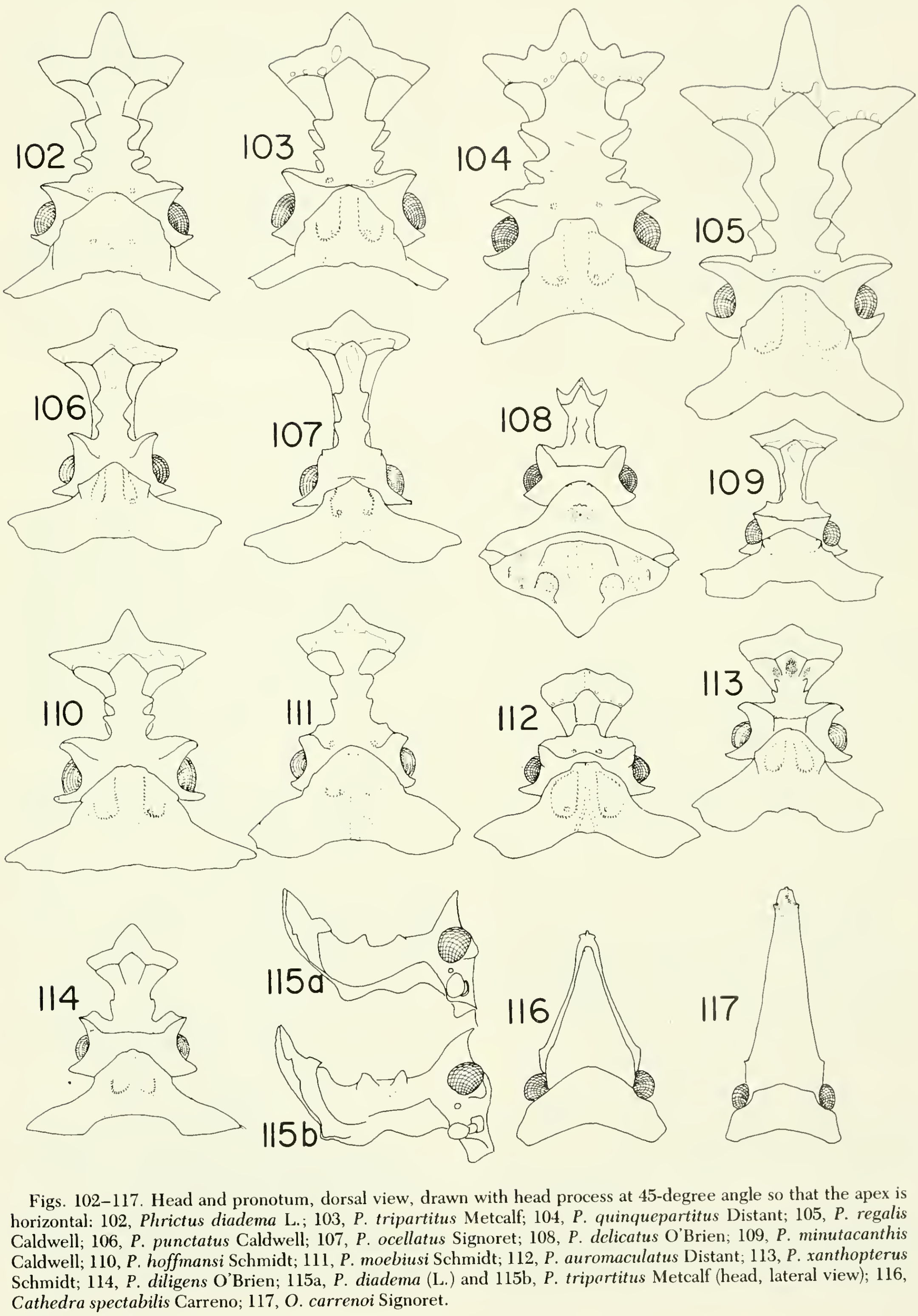
*Phrictus* Spinola 1839:216. Type-species: *Fulgora diadema* Linnaeus by monotypy.

Large, reddish brown or yellowish brown insects, rarely yellow and green, 29–53 mm; head 1/8 to 1/4 length of insect. Head process porrect, terete, usually enlarged into trifurcate apex (Figs. 102–115); dorsolateral carinae each with two pairs of spines, ventrolateral carinae each produced into flange near frontoclypeal suture and into small, dull spine at junction of frons and clypeus. Preocular flange horizontal, small; supra- and postocular flanges produced into strong spines. Tegmen with M not pectinate, cross-veins reticulate in corium forming square cells behind stigmal line. Female with ninth tergite medially shorter than eighth.

These beautiful insects with a name that means "horrible" or "terrible" may be identified by the shape of the apex of the head process and the waxy tufts on it, the color pattern of the tegmina, and the color of the hind wings. Caldwell (1945) also used the median notch in the caudal margin of the pronotum and variation in the furcation of the median carina around the notch, which I found difficult to quantify. The female first valvulae, as he illustrated, also serve to identify difficult specimens. The apex and venter of the head process are usually reddish orange or reddish brown with a white stripe down the dorsum reaching the apex of the pronotum. There are several color patterns on the tegmina which will be discussed under species descriptions. I have illustrated the head process with the insect at approximately a 45-degree angle in order to provide a good view of the apex. Because this makes the length of the head and process difficult to determine, I have included a head length and head/pronotum ratio.

Key to the Species of *Phrictus*

| | | |
|---|---|---|
| 1. | Head process flattened apically, transversely arcuate, lacking definite apical teeth (Fig. 112); base of hind wing yellow with transverse bands of brown maculae ........................................ *auromaculatus* Distant | |
| — | Head process with 3 to 5 apical teeth (Figs. 106–111, 113, 114); hind wing lacking transverse bands of brown maculae ............. | 2 |
| 2(1). | Head process with 5 apical teeth (Fig. 104) .................... *quinquepartitus* Distant | |
| — | Head process with 3 apical teeth ........... | 3 |
| 3(2). | Hind wing with large (ca 2 mm), hyaline, apical spots, visible from below with wing unspread .............................. | 4 |
| — | Hind wing without hyaline, apical spots, but small pruinose areas sometimes present, visible when wings are spread ................ | 5 |
| 4(3). | Hind wings yellow or orange at base; head process with 3 black spots dorsally just behind apical area (Fig. 113) .... *xanthopterus* Schmidt | |
| — | Hind wing red at base; head process with no black markings near apex, but diamond-shaped, red area in same position (Fig. 107) ........................ *ocellatus* Signoret | |
| 5(3). | Basal area of hind wing yellow or yellow-orange .................. *moebiusi* Schmidt | |
| — | Basal area of hind wing red or reddish orange .................................... | 6 |
| 6(5). | Tegmen with continuous, broad, yellow, transverse fasciae present ................ | 7 |
| — | Tegmen lacking transverse fascia, or, if present, interrupted medially ............. | 8 |
| 7(6). | Tegmen brown, transverse fascia yellow only ........................... *diligens*, n. sp. | |
| — | Tegmen scarlet with green veins, anterior edge of fascia partially bordered with black ........................ *tripartitus* Metcalf | |
| 8(6). | Transverse fascia absent, apical trident of head process 2/3 as wide as distance between supraocular spines (Fig. 108) ............. ......................... *delicatus*, n. sp. | |
| — | Transverse fascia interrupted medially; apical trident of head process wider (Figs. 105, 106, 109, 110) ............................ | 9 |
| 9(8). | Head process with apical teeth broader than head (Fig. 105); hind wing with black or fuscous area covering apical three-fourths ..... ......................... *regalis* Caldwell | |
| — | Head process with apical teeth not wider than head (Figs. 106, 109, 110); hind wing with black or fuscous areas covering apical third . | 10 |
| 10(9). | Tegmen green in basal two-thirds, with a few small, round, red or orange maculae; apical third with large, brown spots ............. ....................... *hoffmannsi* Schmidt | |




Figs. 102–117. Head and pronotum, dorsal view, drawn with head process at 45-degree angle so that the apex is horizontal: 102, *Phrictus diadema* L.; 103, *P. tripartitus* Metcalf; 104, *P. quinquepartitus* Distant; 105, *P. regalis* Caldwell; 106, *P. punctatus* Caldwell; 107, *P. ocellatus* Signoret; 108, *P. delicatus* O'Brien; 109, *P. minutacanthis* Caldwell; 110, *P. hoffmansi* Schmidt; 111, *P. moebiusi* Schmidt; 112, *P. auromaculatus* Distant; 113, *P. xanthopterus* Schmidt; 114, *P. diligens* O'Brien; 115a, *P. diadema* (L.) and 115b, *P. tripartitus* Metcalf (head, lateral view); 116, *Cathedra spectabilis* Carreno; 117, *O. carrenoi* Signoret.

— Tegmen brown or reddish brown, sometimes with yellow spots ........................ 11

11(10). Tegmen some shade of reddish brown, with pink, calloused areas present, especially basally; head process toothed on ventral surface (Fig. 115a)........... *diadema* (Linnaeus)

— Tegmen brown, maculate with yellow; head process not toothed ventrally ............. 12

12(11). Combined length of head process and head as long as pronotum; expanse of trifurcate apex equal to distance between ocular spines (Fig. 109)................ *minutacanthis* Caldwell

— Combined length of head process and head longer than pronotum; expanse of apex much greater than distance between ocular spines (Fig. 106) ............... *punctatus* Caldwell

### *Phrictus auromaculatus* Distant
Fig. 112

*Phrictus auromaculatus* Distant 1905:672. Type repository: BMNH.
*Phrictus notatus* Lallemand 1931:188. Type repository: FSAG, NRS. *New synonymy*.

LENGTH.—Male 29–32 mm, female 34–35 mm; head length 3.7 mm; ratio, head/pronotum 1.0.

Head process semicircular at apex, not divided into teeth, orange-red; three round, waxy plates on each side (Fig. 112). Tegmen evenly pale brown mottled with yellow, veins dark brown in corium, no transverse fascia. Hind wings yellow at base, brown posteriorly; two maculate, brown bands from anal area running into yellow area.

This species is easily separated by the apex of the head not being divided into spinelike segments. It may be verified by the yellow base of the hind wings and the evenly colored tegmina.

DISTRIBUTION.—Syntypes: BOLIVIA (*auromaculatus*); ECUADOR (*notatus*). I have seen five other specimens collected from BOLIVIA: Santa Cruz; Prov. Sara [*sic*], 450 m; BRAZIL: Sinop; PERU: Jauja Prov., Satipo.

### *Phrictus delicatus*, n. sp.
Fig. 108

LENGTH.—Female 36 mm; head length 3.7 mm; ratio, head/pronotum 1.3.

Head process tripartite, lateral portions directed anterad, not laterad, smaller than that of *minutacanthis;* head pale brown (Fig. 108). Mesonotum with three pairs of dark spots (pin is placed through apex; there may or may not be one there). Tegmen evenly colored, no fascia. Hind wings red basally, posteriorly pale brown.

This species may be identified by the pale brown, narrow head process, without a white dorsal stripe and red venter and apex. The pale apex of the hind wings separates this species from all but *moebiusi*. The evenly colored tegmen, broader and less rooflike than most of the species, is similar to that of *auromaculatus* and *ocellatus*.

HOLOTYPE (female).—BRAZIL: Amazonas, S. Paulo de Olivenca, VII-32, A. Maller Colln., Frank Johnson Donor (AMNH). The printed label says S. P. Olivenca/ Amazonas/ Brasil VII-32. The handwritten label underneath gives the more complete data.

### *Phrictus diadema* (Linnaeus)
Figs. 102, 115a.

*Fulgora diadema* Linnaeus 1767:703. Type repository: UZIU.
*Phrictus diadema* (Linnaeus), Spinola 1839: 219.

LENGTH.—Male 38 mm, female 45 mm; head length 8 mm; ratio, head/pronotum 2.0.

Apex of head process trifurcate, three or four pairs of lateral, waxy plates and one median oval (Fig. 102). Ventral margin of head process in lateral view sinuate. Hind wings red at base. Tegmina mottled with red and brown in large splotches, transverse, yellowish fascia narrow, not bordered anteriorly in black.

This species most closely resembles *regalis* in the mottled color pattern of the tegmen and pale, transverse fascia and the sinuate ventral margin of the head process in lateral view, but *regalis* has a much wider, trifurcate apex on the head process, exceeding the distance between the tips of the supraocular spines (Fig. 105). In *diadema* the spines and apex are about the same width.

DISTRIBUTION.—Type: INDIA ? [error]. I have seen two other specimens collected in November from BRAZIL: Linhares.

### *Phrictus diligens*, n. sp.
Fig. 114

LENGTH.—Female 40–43 mm; head length 6 mm; ratio, head/pronotum 1.3.

Apex of head process trifurcate, narrow band of waxy plates each side (Fig. 114). Hind wings red at base. Tegmen evenly brown with unbroken clear transverse fascia.

This species may be identified easily by the

brown tegmen with the unbroken transverse band. I name it *diligens*, which means prim, because it is more conservative in color and shape of head process than the other species. It is most closely related to *diadema* and *regalis* in the color pattern of the tegmen.

HOLOTYPE (female).—COLOMBIA: 1,500 ft, Anchicaya, 26-VII-1970, J. M. Campbell (LOB). Paratype (female): COLOMBIA: Dept. El Valle, Anchuaya, 200–300 mi, 27-IV-1969, Gonin-H Balazar-S. Draachsler Rec. (MNHP).

*Phrictus hoffmannsi* Schmidt
Fig. 110

*Phrictus hoffmannsi* Schmidt 1905:338. Type repository: IZW.

LENGTH.—Male 37 mm, female 48 mm; head length 7 mm; ratio, head/pronotum 1.0.

Apex of head process trifurcate, large, squarish, waxy plate area on each side (Fig. 110). Hind wings red at base. Tegmina green mottled with yellowish orange in large splotches, clavus predominately orange, broad, transverse, yellow fascia interrupted by brown spots medially and toward commissure, membrane yellowish brown with brown oval spots.

This species may be distinguished easily by its bright green and yellowish orange tegmen.

DISTRIBUTION.—Holotype (female): PERU: Chanchamayo. I have seen four other specimens collected in January from PERU: Tingo María; ECUADOR: Guayaquil, Loja.

*Phrictus minutacanthis* Caldwell
Fig. 109

*Phrictus minutacanthis* Caldwell 1945:180, pl. 7, Figs. 2, 16, pl. 8, Fig. 2, pl. 9. Type repository: USNM.

LENGTH.—Female 36 mm; head length 4.8 mm; ratio, head/pronotum 1.5.

Apex of head process trifurcate, small; waxy plate on each side; pale red, midline near apex with reddish triangle (Fig. 109). Hind wings red at base. Tegmina light brown evenly mottled with yellow, transverse yellowish fascia indistinct, broken.

This species may be identified by its small head. It resembles *xanthopterus* and *punctatus* most closely in the light brown tegmen with yellow markings, and *ocellatus* and *punctatus* in having the red subapical triangle on the pale dorsum of the head process.

DISTRIBUTION.—Holotype: PERU: Chaquimayo. I have seen only the type.

*Phrictus moebiusi* Schmidt
Fig. 111

*Phrictus moebiusi* Schmidt 1905:335. Type repository: ZMHB.

*Phrictus sordidus* Caldwell 1945:180, pl. 7, Figs. 3, 20, pl. 8, Figs. 1, 13, pl. 9. Type repository: USNM. *New synonymy*.

LENGTH.—Male 40 mm, female 43–48 mm; head length 6 mm; head/pronotal ratio 1.2.

Apex of head process trifurcate, large, waxy plate on apex (Fig. 111). Hind wings yellow at base, posterior pale brown. Tegmina brown evenly mottled with yellow, transverse fascia pale, broad, interrupted by two brown spots in middle and near commissural margin.

This is one of three species with yellow coloration at the base of the hind wing. *P. auromaculatus* has a head process without apical spines, and *xanthopterus* has white spots in the posterior brown area of the hind wing. The type of *sordidus* is a pale specimen that agrees in all external characters with *moebiusi*.

DISTRIBUTION.—Syntype (female): COLOMBIA: Antioquia (*moebiusi*); ECUADOR (male holotype *sordidus*). I have seen four other specimens collected in January from "New Granada" and ECUADOR: Route Mono-Los Banos, km 37, 2,385 m.

*Phrictus ocellatus* Signoret
Fig. 107

*Phrictus ocellatus* Signoret 1855:v. Type repository: NHMV.

LENGTH.—Male 35 mm, female 42 mm; head length 6.0; ratio, head/pronotum 1.9.

Apex of head process trifurcate; large, waxy plates on each side; red diamond and median line along pale dorsum of process (Fig. 107). Hind wings red at base, white spots in brown posterior area. Tegmina evenly mottled with pale yellow and red brown, no fascia.

Two species have hind wings with white spots in the brown posterior area, *xanthopterus* with a yellow base and *ocellatus* with a red base.

DISTRIBUTION.—Holotype (female): COLOMBIA: Fusagasuga. I have seen two other specimens collected in June from VENEZUELA: Rancho Grande.

### *Phrictus punctatus* Caldwell
Fig. 106

*Phrictus punctatus* Caldwell 1940:181, pl.7, Figs. 12, 23, pl. 8, Fig. 6, pl. 9. Type repository: USNM.

LENGTH.—Female 40 mm, head length 6.5 mm; ratio, head/pronotum 1.4.

Apex of head process trifurcate, with transverse, waxy plates; triangular red area on midline behind apex (Fig. 106). Hind wings red at base, pale brown posteriorly. Tegmina brown mottled with yellow in large splotches, clavus predominantly yellow; transverse, yellowish fascia narrow, interrupted medially; diagonal yellow line from clavus to costal margin.

In coloration, the tegmen of *punctatus* most closely resembles *xanthopterus*, while the color of the head process resembles *ocellatus* and *minutacanthis*.

DISTRIBUTION.—Holotype (female): PANAMA: Bugaba. Paratype: El Volcan. I have seen two other specimens, one without data, the other collected from COSTA RICA: Palo Verde.

### *Phrictus quinquepartitus* Distant
Fig. 104

*Phrictus quinquepartitus* Distant 1883:24, pl.4, Fig. 8. Type repository: BMNH.

LENGTH.—Male 40–42 mm, female 45–48 mm; head length 9.3 mm; ratio, head/pronotum 2.06.

Apex of head process trifurcate, one median and three lateral pairs of waxy tufts in apex (Fig. 104). Hind wings red at base. Tegmina red with green veins; transverse, yellowish fascia bordered anteriorly in black.

This species is closely related to *tripartitus* in the color of the tegmen but differs in the apex of the head process.

DISTRIBUTION.—Syntypes: PANAMA: Bugaba, 3,000–4,000 ft; COLOMBIA: Bogota. I have seen nine other specimens collected in February, June, August, October and December from PANAMA: Barro Colorado Island, Cocle, Chiriqui; COSTA RICA: La Selva.

### *Phrictus regalis* Caldwell
Fig. 105

*Phrictus regalis* Caldwell 1945:183, pl. 7, Figs. 7, 19, pl. 8, Fig. 8, pl. 10. Type repository: USNM.

LENGTH.—Male 42 mm, female 49–53 mm; head length 10; ratio, head/pronotum 2.3.

Apex of head process trifurcate, three waxy tufts on each side, two larger ones medially, semicircular carinate area astride median carina (Fig. 105). Hind wings red at base. Tegmina mottled with red and brown in large splotches; transverse, yellowish fascia narrow, not bordered anteriorly in black.

This species is very similar to *diadema* in the color of the tegmen, but the apex of the head process is much wider in *regalis* (Figs. 105, 102).

DISTRIBUTION.—Holotype (female): FRENCH GUIANA: Maroni River, near Duserre. I have seen three other specimens collected in March from FRENCH GUIANA: St. Jean du Maroni; SURINAME: Nassaugebergte.

### *Phrictus tripartitus* Metcalf
Figs. 103, 115b

*Phrictus tripartitus* Metcalf 1938:365, pls. 20, 21. Type repository: AMNH.

LENGTH.—Male 35–40 mm, female 43–45 mm; head length 9.4 mm; ratio, head/pronotum 1.8.

Apex of head process trifurcate, three round, waxy plates and one oval on each side (Fig. 103). Head process sinuate ventrally in lateral view (Fig. 115b). Hind wings red at base. Tegmina red with green veins; transverse, yellowish fascia bordered anteriorly in black.

This species most closely resembles *quinquepartitus* in the color of the tegmen, but the species may be separated by the shape of the apex of the head process. Some specimens of *tripartitus* do have five spines, but the intermediate spines are smaller than those of *quinquepartitus* (Fig. 104) and the shape of the other teeth is like that illustrated for *tripartitus* (Fig. 103).

DISTRIBUTION.—Type: BELIZE. I have seen 21 other specimens collected from August through October from BELIZE: 24 mi SE Belmopan, 10–11 mi S Georgeville; HONDURAS: La Ceiba; MEXICO: Nuevo X-Can [*sic*], San Quintin, Yucatan.

### *Phrictus xanthopterus* Schmidt
Fig. 113

*Phrictus xanthopterus* Schmidt 1910:144. Type repository: IZN.

LENGTH.—Female 39–41 mm; head length 5 mm; ratio, head/pronotum 1.0.

Head process with apex trifurcate, without waxy plates, orange-red, with three triangular, black spots behind apex (Fig. 113). Hind

wings yellow at base with white spots in brown posterior area. Tegmen brown with yellow markings, half of clavus predominantly yellow; transverse, yellow fascia interrupted medially.

This species is one of the most distinctive with the hind wings yellow at base and with white spots in the apical brown area and the three black, subapical spots on the head process. The tegmen most closely resembles *punctatus*.

DISTRIBUTION.—Holotype (female): ECUADOR: Canelos. I have seen six other specimens collected in June and July and December from PERU: Cusco; Sta. Isabel; Route Olmoc-Tarapoto, km 385, 1,800 m; Tingo María; ECUADOR: Lumbagui.

## *Rhabdocephala* Van Duzee

Fig. 23

*Rhabdocephala* Van Duzee 1929:190. Type-species: *R. brunnea* Van Duzee, original designation.

Small, brown, narrow insects, 12–16 mm long; head about 1/3 length of insect. Head process porrect, terete, sides parallel; apex slightly widened; dorsal lateral carinae complete, ventral incomplete, present only in middle of process. Preocular and supraocular flanges absent. Tegmen with M not pectinate, cross-veins reticulate, apical margin angled at apex of clavus, forming angulate, not smoothly rounded, apical margin. Ninth abdominal tergite 1.5 times length of eighth.

These small insects may be separated from other small Fulgoridae by the simple cephalic process with no dorsolateral undulate carinae as in *Scolopsella* and the head process not dorsoventrally flattened as in *Amycle*.

### *Rhabdocephala brunnea* Van Duzee

Fig. 23

*Rhapdocephala brunnea* Van Duzee 1929:191. Type repository: CAS.

LENGTH.—Male 12–14 mm, female 14.5–16 mm; head 5.2 mm; ratio, head/pronotum 2.1.

Tegmen brown mottled with white. Hind wing red in basal third, brown posteriorly.

DISTRIBUTION.—Holotype (female): USA: Arizona. I have seen 15 other specimens collected from May to October from USA: ARIZONA: Pima, Cochise, and Santa Rita counties; MEXICO: Sonora, 15 mi S Hermosillo. Two specimens were collected on *Baccharis sarothroides* Gray.

## *Scolopsella* Ball

Figs. 8–13, 24–25

*Scolopsella Ball* 1905:118. Type-species: *S. reticulata* Ball by original designation.

Small, brown insects, 14–21 mm long, head .23-.28 length of insect. Head process porrect, terete, very slightly enlarged at apex; dorsolateral carinae undulate; median and lateral ventral and marginal carinae complete on process and frons. Preocular flange indistinct. Tegmen with M pectinate (3 branches), commissural margin emarginate between claval apex and wing tip.

This genus of small, brown insects may be separated from other similar genera by the straight head process with dorsolateral margins crenulate or undulate and without the apex greatly expanded. The head process is not as unadorned as *Rhabdocephala*, lacks the transverse wrinkles of *Aphrodisias*, and is not flattened as in *Amycle*. *Diareusa* specimens are much larger insects with much shorter heads.

Key to the Species of *Scolopsella*

1. Length of anal flap of male greater than width at apical expansion (Fig. 23); apical margin of pygofer emarginate ventrally (Fig. 25) ........ ................................ *reticulata* Ball
— Length of anal flap of male less than width at apical expansion (Fig. 20); apical margin of pygofer smoothly convex (Fig. 22) ............ ........................... *mexicana* O'Brien

### *Scolopsella mexicana* O'Brien

Figs. 8–10, 24

*Scolopsella mexicana* O'Brien 1985:73. Type repository: LOB.

LENGTH.—Male 14–15 mm, female 17–21 mm; head length 5.6 mm; ratio, head/pronotum 3.7.

Tegmen various shades of brown, cross-veins and reticulations pale, some apical cells white. Structural characteristics common to both species given in generic description.

*Scolopsella reticulata* and *S. mexicana* may be separated by the shape of the anal flap, which can be seen without dissection, the applicable characters being given in the key. Once males are identified in this way, females may often be associated with them because the golden brown *reticulata* is slightly larger

and the head process is wider, and *mexicana* is darker.

DISTRIBUTION.—Type: MEXICO. I have seen seven other specimens collected from June through September from Baja California.

### *Scolopsella reticulata* Ball
Figs. 11–13, 25

*Scolopsella reticulata* Ball 1905:118. Type repository: CAS.

LENGTH.—Male 14–16 mm, female 17–19 mm; head length 5 mm; ratio, head/pronotum 4.1.

The structural characters and coloration do not differ sufficiently from *S. mexicana* to determine the species without either using the shape of the male anal flap or comparing the two species as discussed above.

DISTRIBUTION.—Holotype: ARIZONA. I have seen other specimens collected from April to November in ARIZONA: Maricopa, Pima, Pinal, and Santa Cruz counties; CALIFORNIA: Joshua Tree National Momument, Riverside or San Bernardino County.

### *Sinuala*, n. gen.
Figs. 43, 46–48

Type-species: *Sinuala stali* O'Brien.

Reddish brown, medium-sized insects, 19–21 mm long, head .12 to .15 length of insect. Head process porrect, terete, enlarged at apex; vertex truncated triangle, basal angle rounded, supraocular lobes variable. Frons with lateral carinae diverging anteriorly to form process; lateral margins expanded near frontoclypeal suture, ridge from lateral carina to margin at this expanded area. Frons and clypeus about in same plane, frons not raised above clypeus; clypeus medially and marginally carinate. Preocular flange lengthened into pleural carina. Pronotum without raised median carina, lateral fossettes and two pleural carinae present; apex of mesonotum with striate triangle, delimited by carinae, not high ridge. Tegmen with M not pectinate, clavus open, longitudinal veins angulate, cross-veins variable. Fore and mid femora expanded. Posterior tibiae with eight lateral spines. Female abdominal tergite nine twice length of eight.

This genus is similar to *Aphrodisias*, from which it differs by the costal margin of the tegmen sinuate and the head process not transversely ridged.

Key to the Species of *Sinuala*

1. Supraocular flange expanded, height equal to width of eye; tegmen with 10 strong tubercles . . . . . . . . . . . . . . . . . . . . . . . . . *tuberculata*, n. sp.

— Supraocular flange smaller than above; tegmen with tubercles evanescent . . . . . . . . . . . . . . . . . . 2

2(1). Vertex as long as broad (Fig. 46); hind wing red at base . . . . . . . . . . . . . . . . . . . . . . . . . . *stali*, n. sp.

— Vertex 1.7 times longer than broad (Fig. 48); hind wing pink at base . . . . . . . . . *schmidti*, n. sp.

### *Sinuala stali*, n. sp.
Fig. 46

LENGTH.—Male 19–20 mm; head 2.3 mm; ratio, head/pronotum 1.4.

Head process short, vertex as long as broad. Hind wing red at base, narrow anterior margin and broad posterior area brown, apical angle brown with some white spots and crossveins.

This species may be easily separated from *tuberculata*, which it resembles in wing color and head length, by the small, supraocular flange of *stali*. I name this species in honor of Carl Stål, who provided a fine basis for generic work in this family.

HOLOTYPE (male).—HONDURAS: Lago Yojoa., 6-VI-1976, J. V. Mankins, coll. (LOB). Paratype (male): EL SALVADOR: Alfredo Martinez Cuestas, no further data (NCSR).

### *Sinuala schmidti*, n. sp.
Fig. 47

LENGTH.—Female 21.5 mm; head 3.3 mm; ratio, head/pronotum 2.2.

Head process elongate, vertex 1.7 times as long as broad. Hind wing pink at base, then white; anal margin pale brown, posterior margin with cells infuscate, veins white; apical third brown with white lines following each cross-vein.

This species may be separated from the others by the long head and the pale base of the hind wings. I name this species in honor of Edmund Schmidt, who had an excellent eye for species and a gift for describing the most significant characters precisely.

HOLOTYPE (female): BELIZE: Corazol, 1 mi NW Corozal, 12-VIII-1977. C. W. and L. B. O'Brien and Marshall (LOB).

### *Sinuala tuberculata*, n. sp.
Figs. 43, 48

LENGTH.—Female 21 mm; head 2.6 mm; ratio, head/pronotum 1.6.

Head process short, vertex with postocular flange raised above vertex equal to width of eye, vertex as long as broad. Hind wing red in basal half, anal area brown, apical 2/5 brown with some white spots and cross-veins. Five strong tuberculations on veins in anterior half of tegmen, five smaller in apical half.

This species may be separated easily from the others by the strong tubercles on the tegmen and the strong supraocular flange.

HOLOTYPE (female): COSTA RICA: P. R. Uhler Colln. (NCSR).

### *Stalubra*, n. gen.
Figs. 1–3, 5, 6

Type-species: *Stalubra brunnea* O'Brien.

Medium-sized, brown or reddish, transparent-winged insects, 19–28 mm long, head .14 to .19 length of insect. Head process terete, gradually narrowing to apex, upturned at apex. Vertex twice as long as broad, elongate medially (Fig. 1). Lateral carinae of frons parallel or diverging toward head process, median carina on process and basal 2/3 of frons; frons only very slightly raised above frontoclypeal suture; lateral margins of frons expanded near apex; weak ridge from lateral carina to lateral margins. Clypeus laterally carinate. Preocular flange reduced to slight tubercle on vertical carina joining marginal carinae of frons and vertex (Fig. 3). Pronotum without median carina raised, fossettes and two pleural carinae present; mesonotal apex not depressed or striate. Tegmen with M pectinate (5–7 branches); clavus open; cross-veins undulate, parallel; no small spines on veins, only on wing margins. Posterior tibiae with six lateral spines. Female abdominal tergite nine shorter than eight.

This genus is similar to *Enhydria* in the compressed, recurved head process and translucent tegmen; however, it lacks the hairs on the veins of the tegmen and the dense, diagonal cross-veins along the costal margin found in *Enhydria*, and the head process is less strongly curved. It differs from *Chilobia* in the vertex being elongate medially, whereas the vertex in *Chilobia* is broader than long and emarginate medially (Figs. 51, 54, 60) or hidden by the recurved head process (Fig. 57).

Lallemand's species *Enhydria rufula* (1966) belongs in this genus, but I cannot tell from his description which it is of two of the three species I have before me. The requested type has not yet arrived, and so these two species will be discussed in Part II.

### *Stalubra brunnea*, n. sp.
Figs. 1–3, 5, 6

LENGTH.—Male 19–22 mm; head 2.6 mm; ratio, head/pronotum 1.9.

Head short, vertex 1.5 times as long as wide. Hind wing clear with brown veins. Tegmen translucent with brown markings and minute red dots along veins, apex pale brown with white circles plus some darker brown spots.

HOLOTYPE (male).—BRASIL [*sic*]: Mato Grosso, Sinop (12°31′S, 55°37′W), X-1975, M. Alvarenga (LOB). Paratypes (25 male): same data (LOB, MZSP); GUYANA: 1 male, Upper Mazaruni River, IX–X-1938, A. S. Pinkus (AMNH).

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Natural History, Chicago, Illinois; FSAG—Faculte des Sciences Agronomiques, Gembloux, Belgium; IZW—Instytut Zoologii PAN, Warsaw, Poland; LOB—Lois O'Brien collection, Tallahassee, Florida; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MHNP—Museum National d'Histoire Naturelle, Paris, France; MRSN—Museo Regionale di Scienze Naturali, Turin, Italy; MZF—Museo Zoologico dell' Universita degli Studie di Firenze, Florence, Italy; MZSP—Muzeo de Zoologia, Universidade de Sao Paulo, Brazil; NCSU—North Carolina State University, Raleigh; NHMV—Naturhistorisches Museum, Vienna, Austria; NRS—Naturhistoriska Riksmuseet, Stockholm, Sweden; OSU—Ohio State University, Columbus; UCB—University of California, Berkeley; UMO—University Museum, Oxford University, Oxford, England; UNAM—Instituto de Biologia and Museo de Zoologia, Universidad Nacional Autonoma de Mexico, Mexico City, D.F.; USNM—United States National Museum, Washington, D.C.; UZIL—Universitets Zoologiska Institut, Lund, Sweden; UZIU—Universitets Zoologiska Institut, Uppsala, Sweden; ZMHB—Zoologisches Museum, Humboldt Universitat, East Berlin, East Germany; ZMUC-Zoologisk Museum, Universitets Copenhagen, Denmark; ZSBS—Zoologische Sammlungen des Bayerischen Staates, Munich, East Germany.

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## LIST OF SPECIES

(Countries are listed from south to north, west before east.)

*Amerzanna* O'Brien, new genus
- *peruana* O'Brien — Peru

*Amycle* Stål
- *amabilis* (Westwood) — Mexico
- *brevis* O'Brien — Mexico
- *grandis* O'Brien — Mexico
- *mankinsi* O'Brien — Honduras
- *pinyonae* Knull & Knull — USA: CA, AZ, NM
- *saxatilis* Van Duzee — USA: CA
- *sodalis* Stål — Mexico, El Salvador
- *tumacacoriae* Knull & Knull — USA: TX, AZ
- *vernalis* Manaee — USA: NC, LA

*Aphrodisias* Kirkaldy
- *cacica* (Stål) — Mexico
- *shaman* O'Brien — Mexico

*Artacie* Stål
- *dufourii* (Signoret), resurrected name — Fr. Guiana, Guyana
- *haemoptera* (Perty) — Brazil

*Cathedra* Kirkaldy
- *serrata* (Fabricius) — Bolivia, Peru, Brazil, Fr. Guiana, Suriname, Colombia, Panama, Costa Rica

*Chilobia* Stål
= *Ecuadoria* Distant, new synonymy
- *cinxia* Stål — Venezuela
- *dichopteroides* (Distant), (Ecuadoria), new combination — Ecuador
- *silena* Stål — Ecuador
- *smaragdina* (Walker) — Venezuela

*Copidocephala* Stål
- *guttata* (White) — Panama, Costa Rica, Guatemala, Mexico
- *merula* Distant — Colombia
  =*melanoptera* (Schmidt), new synonymy
- *viridiguttata* Stål — Columbia, Panama, Costa Rica, Honduras, Mexico
  =*ornanda* (Distant), new synonymy

*Diareusa* Walker
- *annularis* (Olivier) — Peru, Brazil, Fr. Guiana, Suriname, Guyana
- *conspersa* Schmidt — Ecuador, Colombia
  =*dahli* Ossiannilsson, new synonymy
- *imitatrix* Ossiannilsson — Venezuela, Panama, Costa Rica, Belize, Mexico
- *kemneri* Ossiannilsson — Peru

*Ecuadoria*, see *Chilobia*

*Enchophora* Spinola
- *atomaria* Brancsik, see *Cornelia*, teste Lallemand 1959:88
- *dufourii* Signoret, see *Artacie*, teste O'Brien 1985:661
- *ensifera* (Germar), to incertae sedis
- *maculata* O'Brien — Peru
- *nigromaculata* Distant — Bolivia, Peru, Ecuador, Brazil
  =*nigrolimbata* Lallemand
- *pallidipunctata* Lallemand — Bolivia, Peru
- *prasina* Gerstaecker — Bolivia, Peru, Panama, Costa Rica
- *pyrrhocrypta* Walker — Brazil, Guyana, Venezuela
- *recurva* (Olivier) — Suriname, Brazil
  =*bohemani* Stål, new synonymy
- *rosacea* Distant — Panama, Costa Rica, Nicaragua
- *sanguinea* Distant — Ecuador, Colombia, Panama, Costa Rica, Nicaragua, Guatemala
  =*florens* Distant, new synonymy
  =*longirostris* Distant, new synonymy
- *stillifera* (Stål) — Panama, Costa Rica, Honduras, Guyana, Belize, Mexico
- *subviridis* Distant — Panama, Costa Rica
  =*subviridis* var. *distanti* Metcalf
- *tuba* (Germar) — Brazil
- *tuberculata* (Olivier) — Brazil, Fr. Guiana, Suriname, Venezuela
  =*tuberculata* var. *fuscomaculata* Lallemand
  =*parvipennis* Walker, new synonymy
- *uniformis* O'Brien — Peru
- *viridipennis* Spinola — Brazil
  =*eminenta* Schmidt, new synonymy

*Enhydria* Walker
=*Ulubra* Stål, new synonymy
- *cicadina* Gerstaecker — Brazil
- *ferruginea* (Walker) to *Hydriena* (Dictyophariadae)
- *longicornuta* Lallemand — Brazil, Trinidad
- *tessellata* (Walker) — Peru, Brazil
  =*brachialis* (Stål), new synonymy

*Fulgora* L. (New synonymies in this genus are attributed to B. V. Ridout)
- *caerulescens* Olivier, to incertae sedis
- *castresii* Guerin-Meneville — Peru, Panama, Mexico
- *cearensis* (Fonseca) — Brazil, Trinidad
- *crocodilia* Brailovsky & Beutelspacher — Mexico
- *graciliceps* Blanchard — Peru, Bolivia, Brazil
  =*orthocephala* (Fonseca), new synonymy, Ridout
- *lampetis* Burmeister — Bolivia, Peru, Brazil, Panama, Costa Rica, Nicaragua, Honduras
- *laternaria* (Linne) — Brazil, Panama, Honduras, Mexico
  =*servillei* Spinola, new synonymy, Ridout
- *lucifera* Germar — Argentina, Bolivia, Brazil
- *riograndensis* (Fonseca) — Brazil

*Odontoptera* Carreno
- *carrenoi* Signoret — Brazil, Fr. Guiana, Guyana, Panama, Costa Rica, Guatemala, Mexico
- *spectabilis* Carreno — Brazil

*Phrictus* Spinola
- *auromaculatus* Distant — Bolivia, Peru, Ecuador, Brazil

| | |
|---|---|
| =*notatus* Lallemand, new synonymy | |
| *delicatus* O'Brien | Brazil |
| *diadema* (Linnaeus) | Brazil, Fr. Guiana, Suriname |
| =*diadema* var. *walkeri* Metcalf | |
| *diligens* O'Brien | Colombia |
| *hoffmannsi* Schmidt | Peru, Ecuador |
| *minutacanthis* Caldwell | Peru |
| *moebiusi* Schmidt | Colombia |
| =*sordidus* Caldwell, new synonymy | |
| *ocellatus* Signoret | Venezuela, Colombia |
| *punctatus* Caldwell | Panama |
| *quinquepartitus* Distant | Colombia, Panama, Costa Rica |
| *regalis* Caldwell | Fr. Guiana, Suriname |
| *tripartitus* Metcalf | Panama, Honduras, Belize |
| *xanthopterus* Schmidt | Peru, Ecuador |
| *Rhabdocephala* Van Duzee | |
| *brunnea* Van Duzee | USA: AZ, Mexico |
| *Scolopsella* Ball | |
| *mexicana* O'Brien | Mexico |
| *reticulata* Ball | USA: AZ, CA |
| *Sinuala* O'Brien, new genus | |
| *schmidti* O'Brien | Belize |
| *stali* O'Brien | Honduras, El Salvador |
| *tuberculata* O'Brien | Costa Rica |
| *Stalubra* O'Brien, new genus | |
| *brunnea* O'Brien | Brazil, Guyana |
| *rufula* (Lallemand), (*Enhydria*), new combination | Brazil |

# A NUMERICAL TAXONOMIC ANALYSIS OF INTERSPECIFIC MORPHOLOGICAL DIFFERENCES IN TWO CLOSELY RELATED SPECIES OF *CICADA* (HOMOPTERA, CICADIDAE) IN PORTUGAL

J. A. Quartau[1]

ABSTRACT.—*Cicada orni* Linnaeus is among the most common and widespread cicadas in Portugal, and, unless a critical study of the male genitalia is made, it is easily confused with the much less widely distributed *C. barbara lusitanica* Boulard. These species are morphologically very similar and sometimes difficult to separate using existing keys. This study attempts to test the discriminating capabilities of numerical techniques commonly used for classificatory purposes, as well as to discover the most effective characters to distinguish between the two species. For these purposes, cluster analysis and principal component analysis were applied to a sample of 64 male specimens characterized by 40 characters (33 derived from the external morphology and 7 from genitalia). In WPGMA cluster analysis, product-moment correlations gave a better separation between these species than did taxonomic distance coefficients; moreover, the analysis derived from the genital characters alone gave better separation than the analyses based on the 33 external characters. Principal component analysis yielded a clear, interspecific separation along the first axis. The best characters to discriminate between males of the two species were the lengths of the pygofer (and its dorsal spine), the tenth abdominal segment, and the appendages of the latter (which are smaller in *barbara lusitanica*), as well as the width of the shaft of the aedeagus (thinner in *orni*). Finally, the uniformity of the general clustering pattern resulting from the two multivariate techniques suggests the presence of two distinct species, as also clearly indicated by behavioral data.

*Cicada orni* Linnaeus is among the most common and widespread cicadas in Portugal, and, unless a critical study of the male genitalia is made, it is easily confused with the much less widely distributed *C. barbara lusitanica* Boulard (Quartau and Fonseca 1988). As live specimens, however, they are easily distinguished by the male calling songs, which are quite distinct. Oscillograms are found in Claridge et al. (1979) and Boulard (1982), respectively, for *C. orni* and *C. barbara lusitanica.*

The two species are externally very similar and sometimes even difficult to separate by existing keys (e.g., Gómez-Menor 1957). In fact, the main distinguishing character used for their separation has been the presence in *barbara* of only two spots on the cross-veins of the forewings instead of four; however, some specimens of *barbara lusitanica* have the full four spots as they occur in *orni* (Fig. 4).

Boulard (1982), when describing the Portuguese form of *C. barbara*, which he originally named *lusitanica*, provided a good diagnosis of the genital characters of this species. However, no detailed comparison of the two species has been made, nor has any type of multiple-character analysis involving the simultaneous use of several measurements or counts been attempted. It was felt of interest, therefore, to see how far some common techniques of numerical taxonomy would discriminate between this pair of closely related species.

This study was undertaken with two main objectives in mind. The first was to apply current techniques of numerical taxonomy commonly used for classificatory purposes with the aim of testing their general discriminating power with respect to these two species. The techniques chosen were a form of hierarchical cluster analysis and principal component analysis. It is known that apart from the explicit use of the former, principal component analysis can also serve as a cluster technique of great generality and can be used to distinguish pairs of putative morphs as in the classical study of Temple (1968). The second objective was to discover new characters that might help to separate *C. orni* from *C. barbara.*

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## MATERIAL

The data on which this study is based were taken from dried male specimens (OTUs) of 32 *Cicada orni* and 32 *C. barbara lusitanica* (Table 1). These samples were mostly taken by the author in Portugal: all 32 males of *orni* were collected in central Portugal; an equal number of males of *barbara lusitanica* were taken in several areas of Algarve (the southern province of Portugal), where the species appears to be particularly common, with the exception of two specimens only that were collected in Sesimbra (south of Lisbon). The localities and sample sizes are *C. orni:* Alburitel, Vila Nova de Ourém (n = 32); *C. barbara lusitanica:* Carvoeiro (n = 25), Praia da Rocha (n = 4), Serra de Monchique (n = 1), and Sesimbra (n = 2).

TABLE 1. List of specimens (males) of *Cicada orni* Linnaeus and of *C. barbara lusitanica* Boulard investigated (OTUs).

| OTUs | Locality, date of capture, and collector |
|---|---|
| *Cicada orni* | |
| 1–15 | Alburitel, 10.viii.1979, J. A. Quartau |
| 16–32 | Alburitel, vii.1971, J. A. Quartau |
| *C. barbara lusitanica* | |
| 33–34 | Carvoeiro, 14.viii.1966, P. D. Rodrigues |
| 35–38 | Praia da Rocha, 17.viii.1973, J. A. Quartau |
| 39–40 | Carvoeiro, 14.vii.1978, J. A. Quartau |
| 41–47 | Carvoeiro, 30.vii.1978, J. A. Quartau |
| 48–55 | Carvoeiro, 28.vii.1978, J. A. Quartau |
| 56–57 | Carvoeiro, 9.viii-10.ix.1980, L. Mendes |
| 58–59 | Sesimbra, 2.viii.1980, J. A. Quartau |
| 60 | Carvoeiro, 31.vii.1978, J. A. Quartau |
| 61–62 | Carvoeiro, 18.vii.1978, J. A. Quartau |
| 63 | Monchique, 2.ix.1971, F. Carvalho |
| 64 | Carvoeiro, 24.viii.1981, J. A. Quartau |

## METHODS

### Measurements and Counts

Thirty-seven of the 40 characters were measurements; the remaining 3 were counts. Measurements were made using a Wild M3 microscope with a graduated eyepiece and were taken as described in Table 2 or as illustrated in Figures 1–9. Of these 40 characters, 33 refer to external morphology and the remaining 7 to male genitalia.

### Data Analysis

Data processing was carried out on the CDC 6500 computer at the Imperial College Computer Center (University of London) using two multivariate statistical programs developed by Prof. R. G. Davies (Department of Pure and Applied Biology, Imperial College) for cluster analysis and ordination (Quartau and Davies 1983, 1985).

In most analyses, characters were standardized by expressing each state as a deviation from the mean in standard deviation units.

For Q-mode analysis, taxonomic distances as well as product-moment correlations were found and structured by the WPGMA method of cluster analysis (Weighted Pair Group Method with Arithmetic Averaging). Phenograms, expressing the phenetic relationships among the OTUs in a hierarchy of increasingly larger clusters, were thus obtained (Figs. 10–16).

For R-mode analysis, character correlations based on data standardized by OTUs were subjected to principal component analysis (PCA). This ordination method transforms the original characters, generally continuous, correlated characters, into a suite of uncorrelated, composite variables—the principal components (principal axes). In addition to being mutually independent, these components account for maximum variance as follows: the variance along the first axis (i.e., the corresponding eigenvalue) is the maximum possible. The second axis describes the next largest variance orthogonal to (uncorrelated with) the first. The third axis follows similarly but is independent of both first two axes, and so on, for as many axes as one wishes to extract (e.g., Gibson et al. 1984). A transposed matrix of the character loadings was post-multiplied by the standardized data matrix to yield a matrix of OTU projections in the principal component space. Two-dimensional ordination diagrams of the representations of the two species, together with the character loadings (scaled eigenvectors), were thus obtained (Figs. 17–18, Table 3).

## RESULTS

### Phenograms

The seven phenograms resulting from various analyses based on all characters, on the genitalia only, or on the external characters alone are shown in Figures 10–16. The WPGMA clustering technique was followed

TABLE 2. Description of characters: measurements and counts (terminology mostly follows Myers [1928]).

| Character No. | Description |
|---|---|
| 1. | Overall length measured from tip of crown to apical margin of the right forewing with the latter in position of rest alongside the body (Fig. 1). |
| 2. | Length of crown measured along a medial line passing through the median ocellus (Fig. 1). |
| 3. | Minimum distance between the ocular sutures measured along the paired ocelli (Fig. 2). |
| 4. | Medial length of frons measured dorsally as indicated (Fig. 2). |
| 5. | Medial length of pronotum measured dorsally as indicated (Fig. 1). |
| 6. | Medial length of mesonotum measured dorsally from anterior margin to posterior margin of cruciform elevation or scutellum (Fig. 1). |
| 7. | Width of pronotum measured at the level of anterior lateral margins (Fig. 1). |
| 8. | Width of pronotum measured at the level of posterolateral margins (Fig. 1). |
| 9. | Width of crown measured at the level of median ocellus and as indicated (Fig. 2). |
| 10. | Inner distance between the paired ocelli (Fig. 2). |
| 11. | Distance between the right paired ocelli and the right ocular suture as indicated (Fig. 2). |
| 12. | Distance between the base of the left antenna and the left ocular suture as indicated (Fig. 3). |
| 13. | Inner distance between the base of antennae (Fig. 3). |
| 14. | Length of frons as illustrated (Fig. 3). |
| 15. | Length of clypeus as illustrated (Fig. 3). |
| 16. | Length of the exposed part of beak. |
| 17. | Length of dorsal margin of the left fore femur as illustrated (Fig. 5). |
| 18. | Length of ventral margin of the left fore femur as illustrated (Fig. 5). |
| 19. | Length of basal spine in ventral margin of left fore femur as illustrated (Fig. 5). |
| 20. | Length of apical spine in ventral margin of left fore femur as illustrated (Fig. 5). |
| 21. | Distance between tips of the apical and basal spines in the ventral margin of the left fore femur as illustrated (Fig. 5). |
| 22. | Distance from anterior right corner to posterior left corner of left operculum as illustrated (Fig. 6). |
| 23. | Distance from anterior left corner to posterior right corner of left operculum as illustrated (Fig. 6). |
| 24. | Length of right forewing as illustrated (Fig. 1). |
| 25. | Greatest width of right forewing as illustrated (Fig. 4). |
| 26. | Length of subcostal cell ("gancho" cell of Gómez-Menor 1957) in right forewing (Fig. 4). |
| 27. | Length of anterior margin of basal cell in right forewing (Fig. 4). |
| 28. | Length of posterior margin of basal cell in right forewing (Fig. 4). |
| 29. | Maximum width of basal cell in right forewing. |
| 30. | Minimum width of basal cell in right forewing. |
| 31. | Number of apical cells in right forewing. |
| 32. | Number of cells other than apicals of right forewing. |
| 33. | Number of spots in cross-veins of right forewing. |
| 34. | Length of pygofer in lateral view as indicated (Fig. 7). |
| 35. | Overall length of tenth abdominal segment as indicated (Fig. 7). |
| 36. | Overall length of appendages of tenth abdominal segment as indicated (Fig. 7). |
| 37. | Distance in basal curvature of shaft of aedeagus as indicated (Fig. 9). |
| 38. | Width of shaft of aedeagus as indicated (Fig. 9). |
| 39. | Width of shaft of aedeagus in area of curvature as illustrated (Fig. 9). |
| 40. | Medial length of eighth sternite or hypandrium (Fig. 8). |

in all; and Pearson's product-moment coefficient and the taxonomic distance coefficient were used as measures of taxonomic proximity.

(a) Genital analyses

Figures 10 and 11 illustrate a correlation and a distance phenogram, respectively, both based on the seven standardized variables of the male genitalia. Both analyses, notwithstanding their being based on a small number of variables, resulted in two main clusters, one with *C. orni* and the other with *C. barbara lusitanica*. However, in the former phenogram, the cluster of *barbara lusitanica* includes one specimen of *orni* (No. 13).

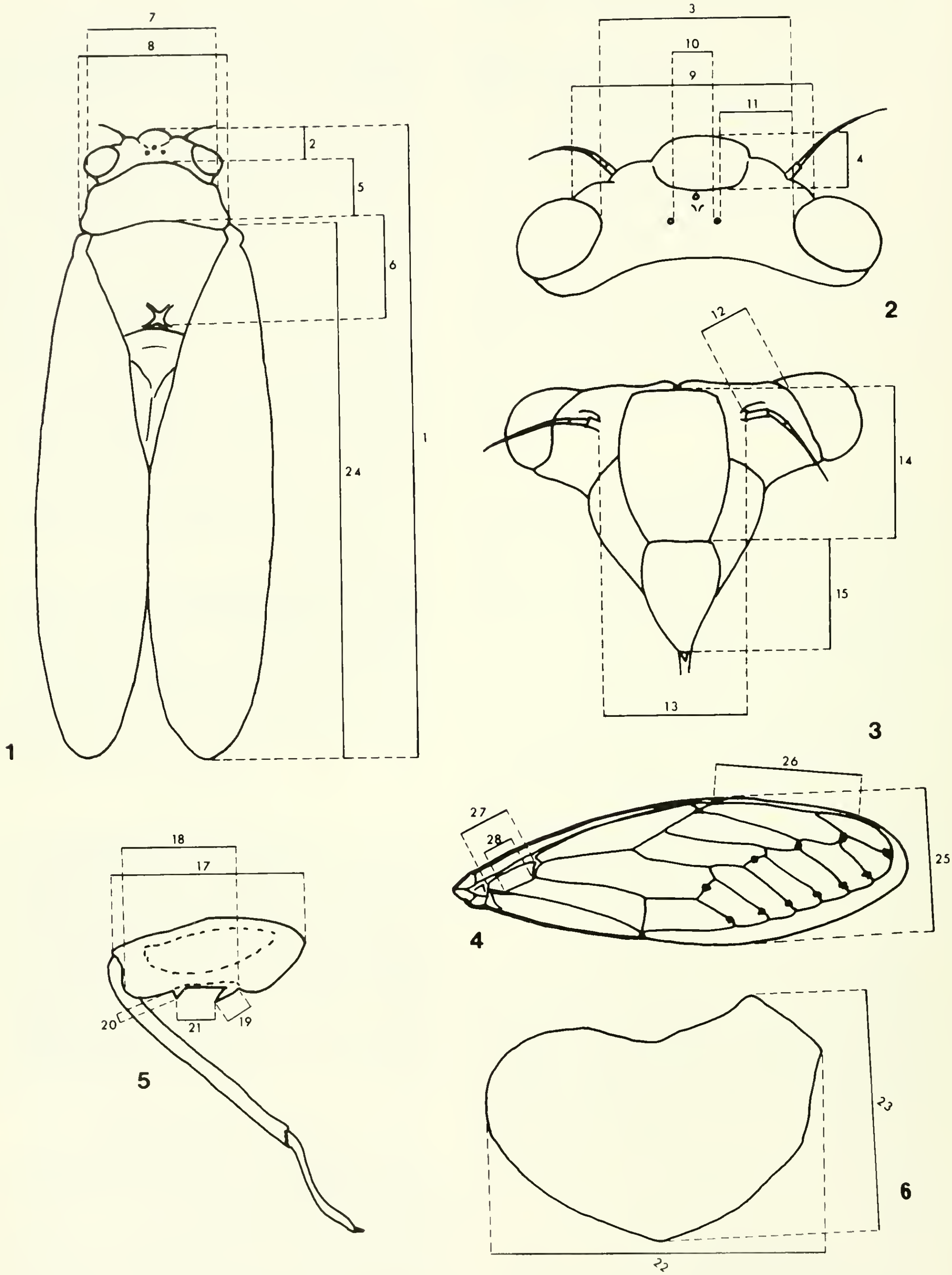
(b) External characters

These analyses resulted in the production of the phenograms depicted in Figures 12 and 13. Both were based on standardized data, but only the correlation coefficient succeeded in giving an almost complete separation of the two species of cicadas. In fact, OTUs were grouped into two main clusters as in the genital analyses, but specimen No. 19 belonging to *C. orni* appeared misplaced within *C. barbara lusitanica* (Fig. 12). On the contrary, the distance phenogram provided much less satisfactory results than the previous analysis, since each of the two major clusters incorporates elements of both species of cicadas (Fig. 13).

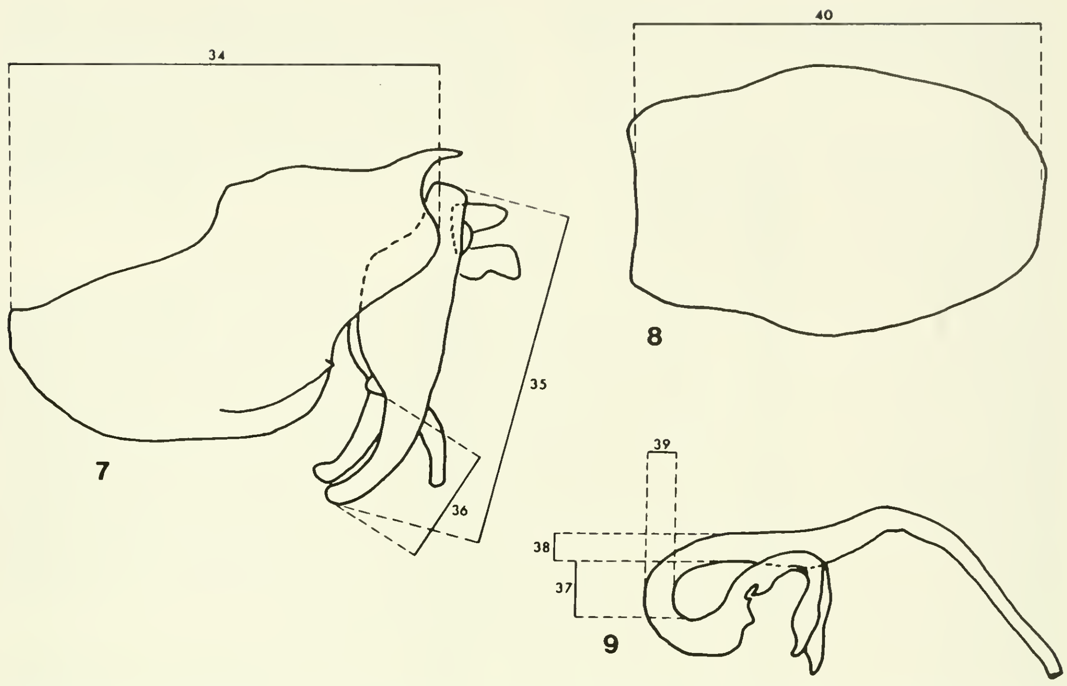
(c) Combined characters

The phenograms of this group of analyses, involving all 40 characters combined, are illustrated in Figures 14–16.

Considering the phenograms based on standardized data (Figs. 14, 16), it is clear that the correlation phenogram gave a much better distinction between the two species than the distance analysis. In fact, the latter (Fig. 16) clustered six specimens of *C. orni* with *C.*




Figs. 1–6. Diagrams of a male *Cicada orni* Linnaeus illustrating most of the measurements taken: 1, body, dorsal view; 2, head, dorsal view; 3, head, anterior view; 4, right forewing, dorsal view; 5, left foreleg, inner view; 6, left operculum, ventral view.




Figs. 7–9. As in Figures 1–6: 7, pygofer and tenth abdominal segment, ventral view; 8, eighth sternite or hypandrium, ventral view; 9, aedeagus, lateral view.

*barbara lusitanica*. Even when the data were unstandardized, correlations gave a good picture of the relationships between these two species (Fig. 15).

## Principal Component Analysis

This analysis involved all 40 characters and was computed from a between-character correlation matrix based on data standardized by OTUs.

As in similar analyses carried out with leafhoppers of the genus *Batracomorphus* (Quartau 1983), slightly more than half (54%) of the total variation in the study was explained by the first three axes.

The first component accounted for 38.90% of the variation in the data and is interpreted as a contrast between the lengths of the pygofer, tenth abdominal segment, or appendages of the latter and the width of the shaft of the aedeagus. It does not represent overall size as commonly is the case, since many of the characters (Table 3) are not positively correlated with it (e.g., Jolicoeur and Mosimann 1960, Blackith and Reyment 1971, Baker 1980, Gibson et al. 1984, Shea 1985). In fact, it must represent both size and shape as has been pointed out by several authors (Mosimann 1970, Oxnard 1978, Humphries et al. 1981). A complete separation of *C. orni* and *C. barbara lusitanica* was given by the discrimination afforded by this axis, which is probably close to the orientation of the optimum discriminant function. The characters loading most heavily on this component (Table 3) are therefore of considerable taxonomic interest, since they are diagnostic for this pair of species. The highest negative scores, in decreasing order, were for characters numbered 35 (length of tenth abdominal segment), 34 (length of pygofer), and 36 (length of appendages of tenth abdominal segment). The highest positive score was for character numbered 38 (width of shaft of aedeagus).

The second principal component accounted for 8.51% of the total variation and was interpreted as a contrast between the number of spots in cross-veins of the wings and the width of the crown. It was most heavily loaded, negatively and positively, on characters numbered 33 and 9, respectively.

The third principal component accounted for 6.61% of the total variation and was interpreted as a factor resulting from the lengths of

TABLE 3. Eigenvector matrix (character loadings) in a principal component analysis of the matrix of correlations among the 40 variables (data standardized by OTUs.)

| Variables | | Scaled eigenvectors | | |
|---|---|---|---|---|
| | | I | II | III |
| 1 | | 0.296 | −0.158 | 0.441 |
| 2 | | 0.404 | 0.123 | 0.155 |
| 3 | | 0.531 | 0.557 | −0.174 |
| 4 | | 0.843 | −0.160 | 0.126 |
| 5 | | 0.492 | 0.300 | −0.119 |
| 6 | | 0.037 | −0.096 | 0.280 |
| 7 | | 0.567 | 0.280 | −0.069 |
| 8 | | 0.314 | 0.365 | −0.131 |
| 9 | | 0.336 | 0.633 | −0.133 |
| 10 | | 0.738 | −0.237 | −0.000 |
| 11 | | 0.687 | 0.155 | −0.200 |
| 12 | | 0.859 | −0.127 | −0.142 |
| 13 | | 0.313 | 0.423 | 0.414 |
| 14 | | 0.117 | 0.422 | 0.306 |
| 15 | | −0.604 | −0.196 | −0.120 |
| 16 | | −0.769 | 0.104 | −0.192 |
| 17 | | −0.316 | 0.338 | 0.524 |
| 18 | | −0.667 | 0.174 | 0.375 |
| 19 | | 0.565 | 0.252 | −0.091 |
| 20 | | 0.531 | −0.066 | 0.111 |
| 21 | | −0.132 | 0.019 | 0.257 |
| 22 | | 0.784 | 0.203 | 0.160 |
| 23 | | 0.847 | 0.112 | 0.000 |
| 24 | | 0.524 | −0.340 | 0.060 |
| 25 | | 0.683 | −0.104 | 0.154 |
| 26 | | 0.187 | −0.207 | −0.412 |
| 27 | | −0.334 | 0.126 | −0.561 |
| 28 | | 0.133 | 0.117 | −0.549 |
| 29 | | −0.011 | −0.207 | 0.471 |
| 30 | | 0.129 | −0.287 | 0.511 |
| 31 | | 0.818 | −0.490 | −0.049 |
| 32 | | 0.818 | −0.479 | −0.059 |
| 33 | | 0.266 | −0.745 | −0.163 |
| 34 | | −0.952 | −0.011 | −0.040 |
| 35 | | −0.958 | −0.153 | −0.001 |
| 36 | | −0.944 | −0.180 | 0.043 |
| 37 | | −0.869 | −0.250 | 0.028 |
| 38 | | 0.942 | −0.065 | −0.023 |
| 39 | | 0.892 | −0.249 | 0.024 |
| 40 | | −0.858 | −0.125 | −0.090 |
| Latent roots | | 15.559 | 3.406 | 2.644 |
| Percentage of variation | component | 38.898 | 8.514 | 6.609 |
| | cumulative | 38.898 | 47.412 | 54.021 |

the anterior and posterior margins of the basal cell of the wings. It was most heavily loaded (negative scores) on characters numbered 27 and 28.

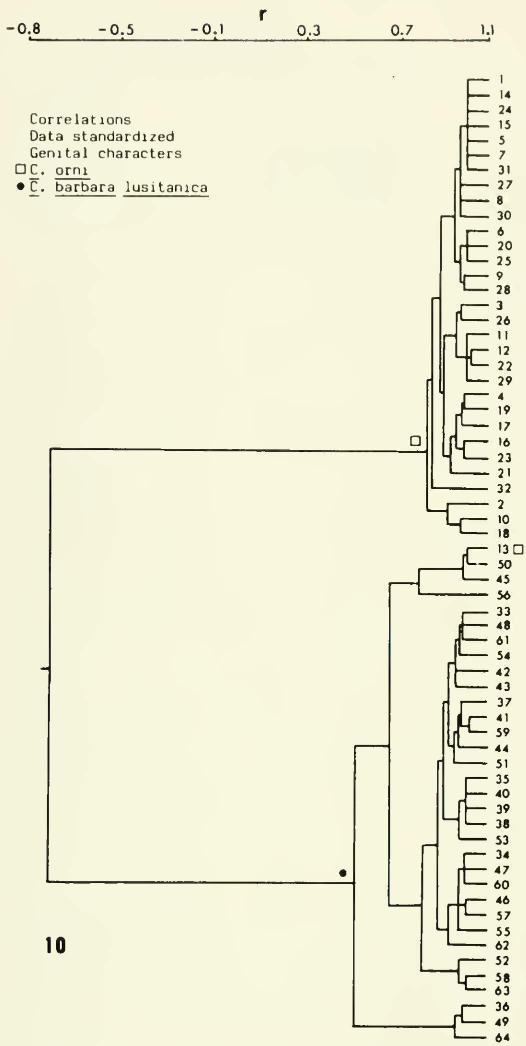
Neither the second nor the third axis leads to a separation of the two species of cicadas. Figures 17 and 18 are two-dimensional views of the relationships among specimens of both species in the space determined by component I combined with component II and by component I with component III, respectively. It is clear that these two plots gave a good separation between *C. orni* and *C. barbara lusitanica*. The plot combining axes II and III did not, however, succeed in giving a correct assignment of the two species and therefore was not illustrated here.

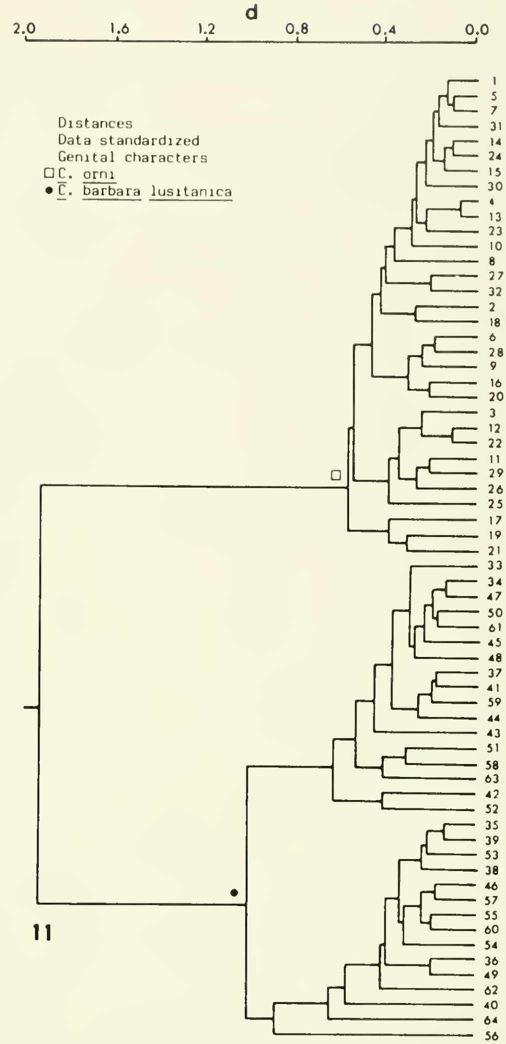
## CONCLUSIONS

Cluster analysis and principal component analysis are two of the methods most commonly used for recognition of group structure in numerical taxonomy (e.g., Quartau 1987). This study suggests that the two general methods are also very useful for discriminating between pairs of closely related species. In fact, because of the uniformity of the general clustering pattern that resulted from the application of both methods, it is clear that two distinct species exist, a fact also indicated by behavioral data.

However, concerning cluster analysis, it is worthwhile noting that the hierarchical structure within each of the two major groups of OTUs differs a good deal from one particular method to another. Moreover, it appeared that correlations were more effective than taxonomic distances in describing relationships between the two cicadas, a result in keeping with Boyce (1964) or Cheetam (1968), for instance. It is interesting to note, in this regard, that such finding is in disagreement with a similar study carried out with leafhoppers (Quartau and Davies 1983) or with results based on other groups (e.g., Smith 1972). Finally, the failure of the cluster analysis using distances with nongenital characters shows that the use of such techniques needs to be undertaken with care and that it might be best to use a consensus of several clustering techniques when applying numerical methods to a novel taxonomic situation.

Principal component analysis succeeded in giving a good distinction of the two species along axis I, in spite of its accounting for only 38.90% of the total variation. This analysis also showed that the main distinguishing characters between *C. orni* and *C. barbara lusitanica* are the following: lengths of the pygofer, the tenth abdominal segment, and the appendages of the latter (which are smaller in *C. barbara lusitanica*, Figs. 19, 22), as well as the width of the shaft of the aedeagus (which is




Figs. 10–11. 10, correlation phenogram based on the seven genital characters with standardized data; 11, distance phenogram based on the seven genital characters with standardized data.

thinner in *orni*, Figs. 20, 23). Moreover, detailed examination of the male genitalia also showed that the dorsal spine of the pygofer is smaller in *barbara lusitanica* than in *orni* (Figs. 19, 22).

## ACKNOWLEDGMENTS

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Figs. 12–13. 12, correlation phenogram based on the 33 external morphological characters with standardized data; 13, distance phenogram based on the 33 external morphological characters with standardized data.

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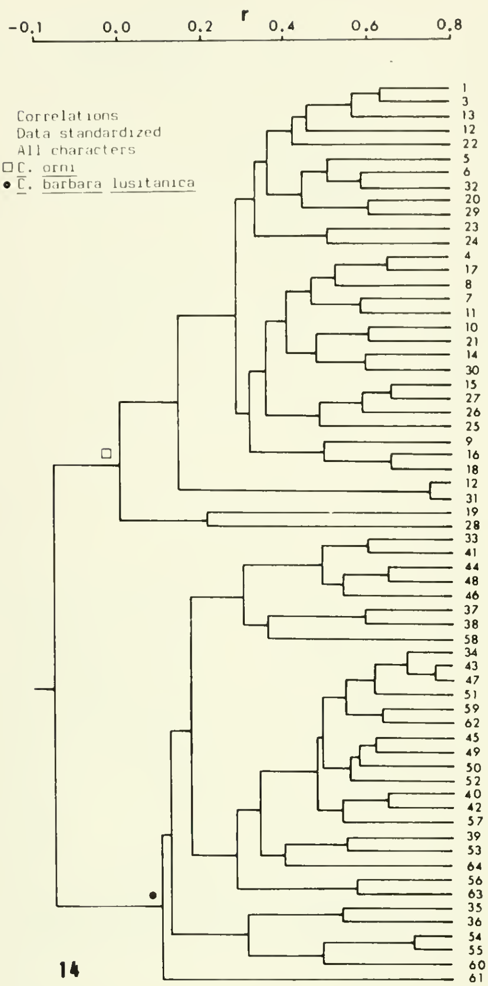


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Figs. 14–15. 14, correlation phenogram based on all 40 combined characters with standardized data; 15, correlation phenogram based on all 40 combined characters with unstandardized data.

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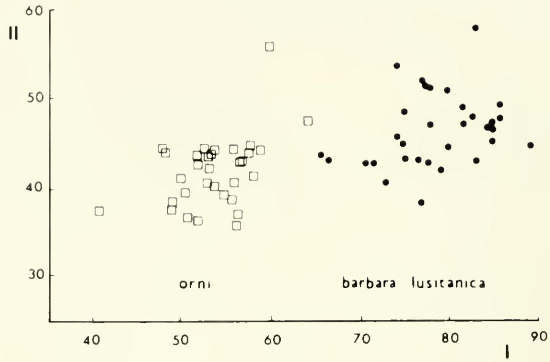


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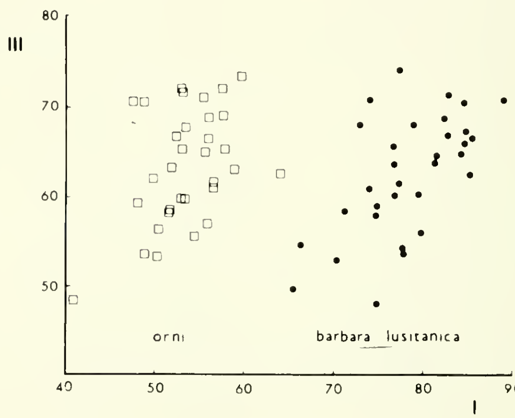


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Figs. 16–18. 16, distance phenogram based on all 40 combined characters with standardized data; 17, a two-dimensional view of the relationships among the 64 OTUs in a space determined by component I on x-axis (38.90%) and component II on y-axis (8.51%) of a principal component analysis of the matrix of correlations among all 40 characters with standardized data; 18, as in Fig. 17 but referred to component I on x-axis and III on y-axis (6.61%).

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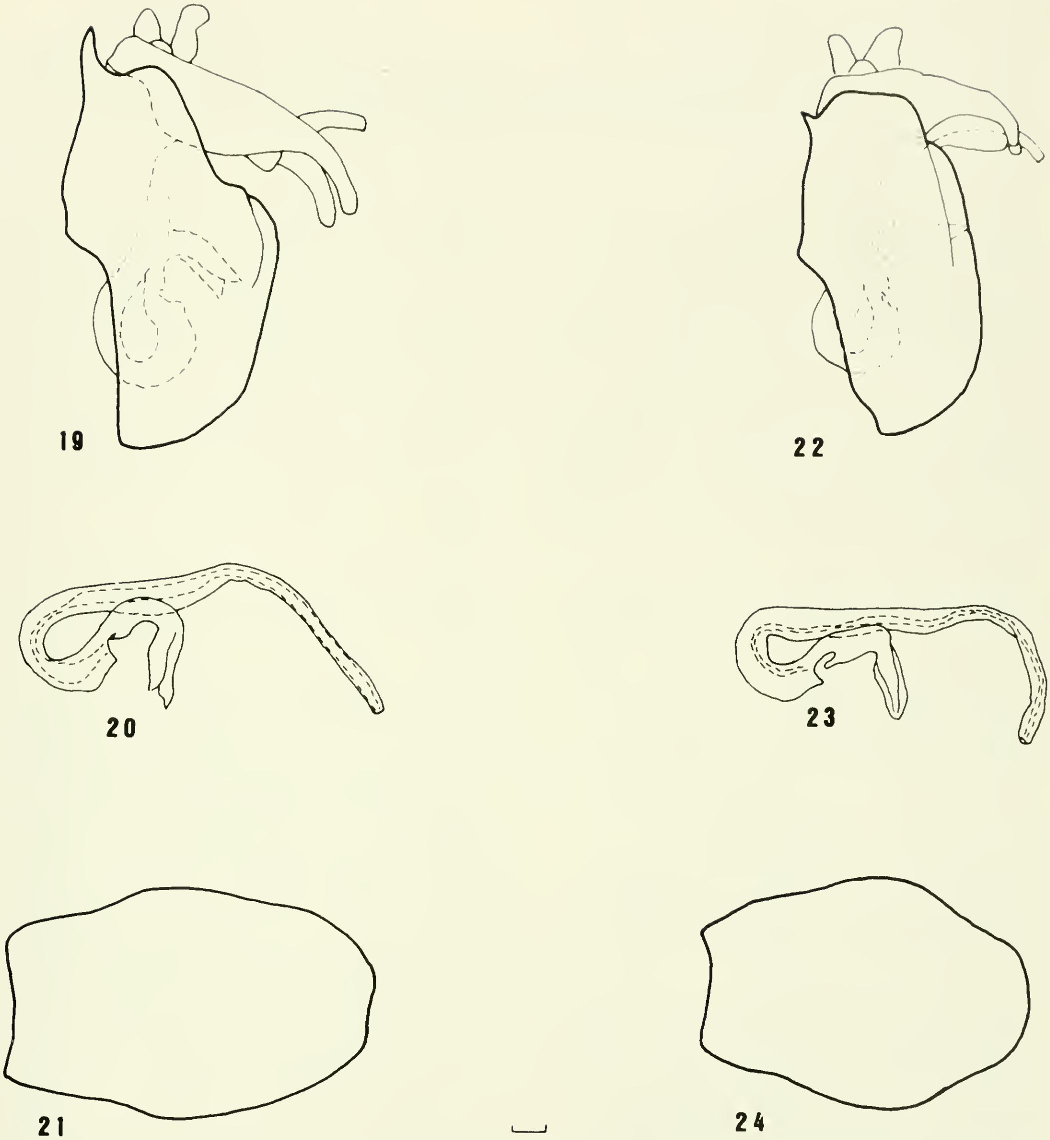


Figs. 19–24. Diagrams of the male genitalia of *Cicada orni* (Figs. 19–21) and of *C. barbara lusitanica* (Figs. 22–24): 19, 22, pygofer and tenth abdominal segment, lateral view; 20, 23, aedeagus, lateral view; 21, 24, eighth sternite or hypandrium, ventral view (scale = 0.5 mm).

# REVISION OF THE NIRVANINAE (HOMOPTERA: CICADELLIDAE) OF THE INDIAN SUBCONTINENT

C. A. Viraktamath[1] and C. S. Wesley[2]

ABSTRACT.—Three tribes of Nirvaninae, namely, Balbillini (two genera and three species), Nirvanini (five genera and 26 species), and Occinirvanini (one genus and one species), occur on the Indian subcontinent. The tribes, genera, and species are redescribed, illustrated, and keyed. New taxa recognized are *Balbillus indicus* n. sp. (India: Kerala), *Stenotortor subhimalaya* n. sp. (India: West Bengal), *Kana bispinosa* n. sp. (India: Tamil Nadu), *K. nigropicta* n. sp. (India: Kerala), *Sophonia bakeri* n. sp. (India: Karnataka, Kerala, Tamil Nadu, Uttar Pradesh; Nepal), *S. bifida* n. sp. (India: West Bengal), *S. complexa* n. sp. (India: Meghalaya), *S. complicata* n. sp. (India: Mizoram, Meghalaya), *S. keralica* n. sp. (India: Kerala), *Nirvana peculiaris* n. sp. (India: Mizoram, Meghalaya), and *N. striata* n. sp. (India: West Bengal, Uttar Pradesh, Himachal Pradesh). The genus *Quercinirvana* Ahmed & Mahmood (type species: *Q. longicephala* Ahmed & Mahmood) is treated as a junior synonym of *Sophonia* Walker. *Kana signata* Distant and *Nirvana greeni* Distant are suppressed as junior synonyms of *K. illuminata* and *N. linealis*, respectively, and are transferred to *Sophonia*. Three other species transferred to *Sophonia* are *Kana modesta* Distant, *Quercinirvana longicephala* Ahmed & Mahood, and *Nirvana insignis* Distant. The relationships among various genera are discussed briefly. The genera *Crispina* Distant and *Mohunia* Distant are excluded from Nirvaninae.

The Nirvaninae, one of the smaller subfamilies of the leafhopper family Cicadellidae, include a predominantly tropical group of leafhoppers. They are fragile, often brightly colored, depressed leafhoppers and common on lush green vegetation. They are often mistaken for Typhlocybinae, but the structure of the head and the more depressed form and truncate basitarsus of the hind leg distinguish Nirvaninae. The subfamily includes 111 species (excluding Mukariinae and other non-Nirvaninae genera, which were traditionally included in the Nirvaninae) distributed in the Oriental (56), Afrotropical (24), Neotropical (7), Palearctic (7), Australian (11), and Pacific island (6) regions. The fauna of Afrotropical (Linnavuori 1979), Australian (Evans 1966), Papua New Guinea (Evans 1973), Neotropical (Kramer 1964), and Palearctic (Kuoh and Kuoh 1983) regions have recently been revised. The tribe Mukariini earlier included in the subfamily by Distant (1908g) and Metcalf (1963) is now considered a subfamily distinct from Nirvaninae (Linnavuori 1979).

Information on host plants of Nirvaninae is very meagre. *Nirvana pallida* Melichar and *N. suturalis* Melichar are destructive to sugarcane and grasses in Taiwan (Schumacher 1915a). They also feed on rice, mulberry, and camphor tree (Esaki and Ito 1954a). Baker (1923a) found *Stenotortor inocarpi* Baker on Otaheite chestnut, *Inocarpus edulis*, in Singapore. In Australia, Nirvaninae feed on *I. edulis*, casuarina, and croton (Evans 1941f). *Tecomaria capensis* is recorded as the host of *Narecho tecomariae* Theron in South Africa (Theron 1970). *Quercinirvana longicephala* Ahmed & Mahmood feeds on *Aesculus indica*, *Quercus dilatata*, and *Viburnum nervosum* (Ahmed and Mahmood 1970). *Chudania delecta* Distant breeds on *Ficus carica* (Ahmed and Mallik 1972). In South America, *Tahura fowleri* Kramer is found on *Passiflora* (Kramer 1964). Kuoh and Kuoh (1983) recorded *Camellia sinensis, Acacia confusa, Citrus reticulata, Pterocarpus indicus, Oryza sativa, Psidium guajava,* and *Chimonanthus praecox* as host plants of species of *Pseudonirvana* Baker (=*Sophonia* Walker) in China. *Nirvana pallida* and *N. greeni* Distant breed on black gram, green gram, cowpea, field bean, pigeon pea, and soybean in India (Ramakrishna 1980).

The Nirvaninae of the Indian subcontinent consist of eight genera and 30 species grouped in three tribes, namely, Balbillini, Nirvanini, and Occinirvanini. The genera *Mohunia* Distant and *Crispina* Distant are excluded from the study, as they probably belong to the subfamily Deltocephalinae.

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## MATERIAL AND ABBREVIATIONS

This study was based mainly on specimens collected over the years and deposited in the insect collection of the Department of Entomology, University of Agricultural Sciences by the senior author and his students. Additional specimens were borrowed from various institutions for the study. Abbreviations used for these institutions and for the depositories of the types of new taxa are as follows:

BMNH – British Museum (Natural History), London.
IARI – Indian Agricultural Research Institute, New Delhi.
IRSNB – Institute Royal des Sciences, Naturelles de Belgique, Bruxelles.
JU – Department of Biosciences, Jammu University, Jammu.
PAU – Punjab Agricultural University, Ludhiana.
UAS – University of Agricultural Sciences, Bangalore.
USNM – U.S. National Museum (Natural History), Washington, D.C.
ZMHU – Museum für Naturkunde der Humboldt, Universität zu Berlin, Berlin.
ZSI – Zoological Survey of India, Calcutta.

Distant (1908g, 1918b) did not mention the number of specimens (syntypes) of each new species he described, except when a single specimen was involved, viz., *Chundania delecta* Distant (1908g: 268) In this study lectotype designations were made even though a single specimen of the type series (syntypes?) was present in the BMNH collection. Unless otherwise stated they were considered as part of the syntype series.

The terminology used for describing hind leg spinulation follows Davis (1975).

## DESCRIPTION OF TAXA

### Nirvaninae

Delicate, fragile, depressed, small to moderately large (4.0–9.0 mm) leafhoppers. Usually yellow or white, often marked with red, black, orange, or brown fascia. Head as wide as or wider than pronotum. Vertex usually flattened, strongly produced, and with rugae or sculpturing on lateral and anterior regions. Ocelli on crown along lateral margin in front of eyes. Frontoclypeus and clypellus either flat or tumid, in the latter case often provided with a median keel. Lora often small, extreme anterior margin of genae bluntly prominent, extending beyond apex of clypellus. Antennal pits deep, antennal ledges more or less strong, antennae long. Lower margin of eyes sinuate ventrally. Anterior tentorial branches L-shaped. Lateral margins of pronotum carinate (except in *Omaranus* Distant), moderately long. Forewing venation reduced, without cross-veins at base (except Balbillini), longitudinal veins represented by a series of paired pits basally, appendix either narrow (Nirvanini) or broad (*Balbillus* Distant). Hindwing with three or four apical cells, veins 1A and 2A fused basally. Fore and middle tibiae cylindrical or flattened (Balbillini), hind femoral spinulation 2+1+1 (Nirvanini), 2+1+0 (Balbillini and Occinirvanini), or 2+0+0 (Balbillini).

Male pygofer either cylindrical or depressed, with or without anal collar process, but may be armed with ventral process, heavily macrosetose. Valve small, fused with pygofer laterally. Plates usually parallel-sided. Style variable. Connective Y-shaped (Nirvanini) or platelike (Balbillini). Aedeagus with single shaft and often provided with processes.

Linnavuori (1979) suggested that the subfamily Nirvaninae is a derivative of the Aphrodinae–Cicadellinae stock and that Nirvanini is the most advanced tribe.

#### Key to Tribes

1. Fore and middle tibiae flattened; head notched in front of eyes so that the scape is visible in dorsal aspect ........................ Balbillini
— Fore and middle tibiae rounded; scape not visible from above ............................ 2
2(1). Ocelli nearer to apex of head than to eyes; forewing appendix wide and extending around apical wing margin; lora large; vertex about half as long as wide, obliquely produced in front of eyes, with hind femoral spinulation 2+1+0; hind basitarsus with six platellae ... Occinirvanini
— Ocelli nearer to eyes than to apex of head; forewing appendix narrow and does not extend around apex of wing; lora small; vertex as long as wide or longer, not obliquely produced in front of eyes; hind femoral spinulation 2+1+1; hind basitarsus with two or three platellae .. Nirvanini

### Tribe Balbillini

This tribe has been well characterized by Linnavuori (1979). The following additional characters are noted. Forewing with supernumerary cross-veins along costal margin and with two m-cu cross-veins, four to five apical cells, two anteapical cells, and appendix (absent in *Stenotortor* Baker). Hindwing with four apical cells. Hind femoral spinulation

$2+2+0$ or $2+0+0$. Male connective long and incrassate or lamellate and fusiform. Aedeagus simple with large gonopore.

Key to Genera of Balbillini

1. Forewing with a well-developed appendix; hind femoral spinulation $2+1+0$ ...... *Balbillus* Distant
— Forewing without an appendix; hind femoral spinulation $2+0+0$ ............... *Stenotortor* Baker

## Genus *Balbillus* Distant

*Balbillus* Distant 1908g: 287. Type species: *Balbillus granulosus* Distant, by original designation and monotypy.

Head narrower than pronotum. Crown bluntly, angularly produced, convex, declivous anteriorly, with median and submarginal, anterior carinae between ocelli. Face horizontal, flat. Clypellus twice as wide at base as at apex; lora small. Lateral margins of head in front of eyes notched, exposing scape of antenna. Pronotum declivous laterally, with two lateral, carinate margins; mesepisternum attaining lateral position in front of base of wing and strongly ridged. Fore and middle tibiae angular; hind femoral spinulation $2+1+0$, inner spine very slender and minute. Apex of hind basitarsus with three platellae. Hind tibial spinulation $R_1$ $12 \pm 1$, $R_2$ $19 \pm 1$, $R_3$ $25 \pm 1$, $R_4$ $25 \pm 1$.

Pygofer much shorter than its height, without processes. Anal tube short. Genital plate parallel-sided, 3.4 times as long as wide with uniseriate, submarginal setae and few hairlike setae. Apophysis of style simple, without preapical lobe. Connective lamellate and fusiform. Aedeagus articulate with connective, simple and with large gonopore.

REMARKS.—As pointed out by Linnavuori (1979) and Baker (1923), *Balbillus* and *Stenotortor* are closely related. They can be separated by the characters used in the key. The bodies of both genera remain appressed to the leaf surface, which explains the flat nature of the tibiae and the undersurface of the body.

The Indian species, *B. granulosa* and *B. indica*, have hind femoral spinulation $2+1+0$ and three platellae at the apex of the hind basitarsus. The male plate of *B. indica* is parallel-sided. The connective and aedeagus are articulated rather than fused. The connective is spindle-shaped, lamellate rather than long and incrassate, and the preapical lobe of the style is wanting. These characters strongly suggest that the Afrotropical species of *Balbillus*, namely, *B. abas* Linnavuori and *B. trimaculatus* Linnavuori, may not belong to *Balbillus*.

Key to Species of *Balbillus*

1. Vertex and scutellum with dark brown spots .... .............................. *granulosus* Distant
— Vertex and scutellum immaculate ... *indicus*, n. sp.

## *Balbillus granulosus* Distant

Figs. 1–5

*Balbillus granulosus* Distant 1908g: 288. Holotype ♀, Sri Lanka (BMNH, examined).

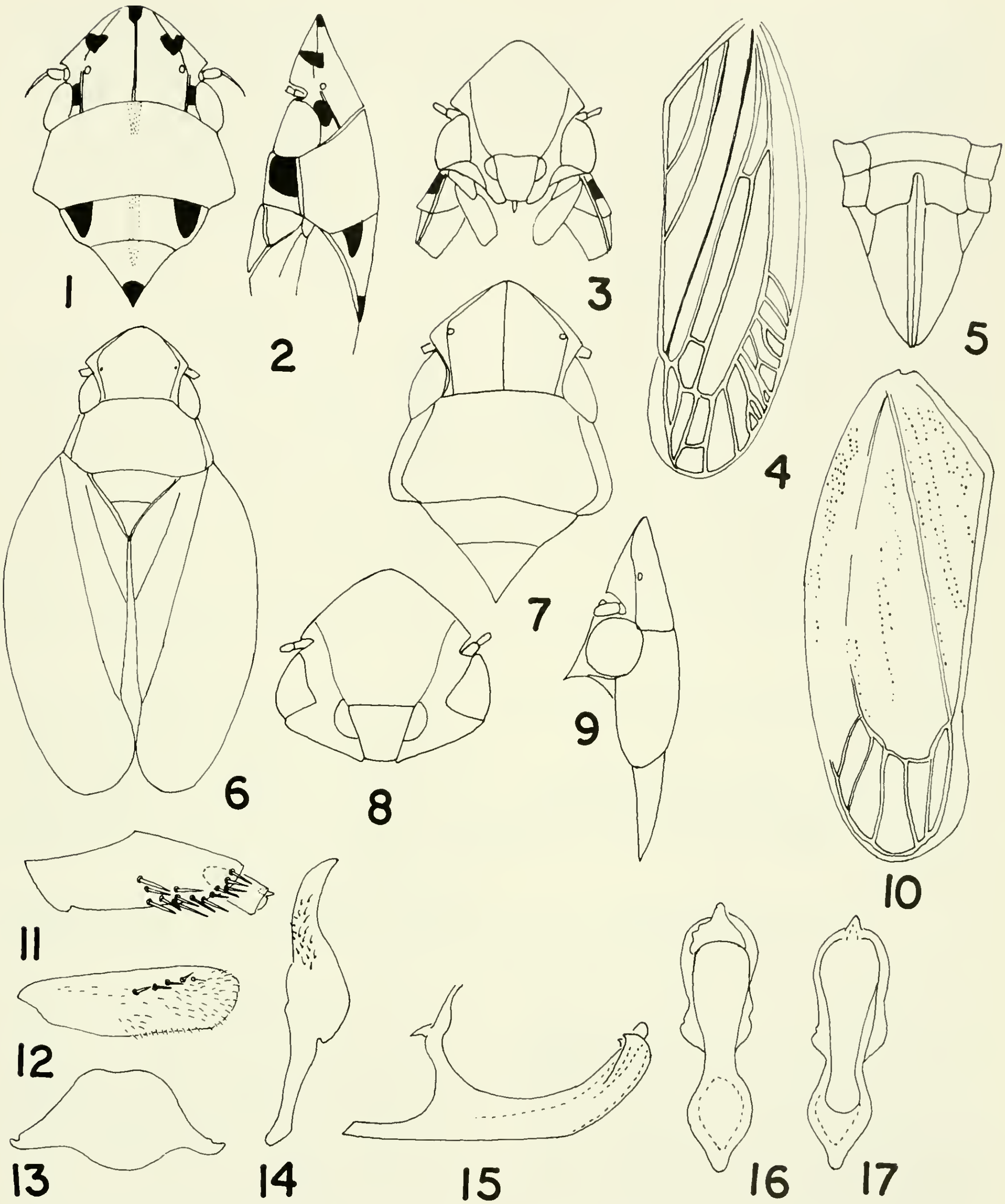
Yellow. Vertex with a median spot, a spot in apical half on either side divided by carina, and a spot near inner margin of eye dark brown. Pronotum with a median, short stripe on anterior margin fuscous. Basal triangles on scutum and apex of scutellum dark brown; blackish, median line on scutellum not reaching apex of scutellum. Longitudinal veins and claval veins lemon yellow, entire surface of forewing punctate, punctations along radial vein and on outer apical cell and a spot at base of appendix fuscous.

Vertex bluntly conical, 1.24 times as wide between eyes as its median length, median carina prominent in its apical half, apical 0.75 of disc sculptured, basal 0.25 polished. Face about as long as wide. Pronotum widened posteriorly. Scutellum longer than pronotum, transversely, finely rugulose beyond sulcus. Forewing 3.4 times as long as wide, with one m-cu cross-vein abut 0.33 distance from base and another near apex limiting the short, inner anteapical cell, outer anteapical cell open behind, numerous veins arising from apical half of outer anteapical cell and reaching costa, few of them forked at costal margin, third apical cell divided by cross-vein. Hindwing with four apical cells.

FEMALE GENITALIA.—Seventh sternum about twice as long as sixth, its hind margin slightly concave with a strong, U-shaped, median excavation, very finely, transversely rugulose. Ovipositor exceeding pygofers.

MEASUREMENTS.—Female 7.10 mm long, head 1.85 mm wide, pronotum 1.87 mm wide.

SPECIMEN EXAMINED.—Holotype ♀ labeled /Type/ /*Balbillus granulosus* Dist., type/ /Ceylon (Green)/ /Distant Coll., 1911–383/ (BMNH).




Figs. 1–17. Species of *Balbillus*. *B. granulosus* Distant: 1, head and thorax; 2, same, profile; 3, face and part of prothorax; 4, forewing; 5, ovipositor. *B. indicus*, n. sp.: 6, general habitus; 7, head and thorax; 8, face; 9, head and thorax, profile; 10, forewing; 11, pygofer; 12, male plate; 13, connective; 14, style; 15, 16, 17, aedeagus, lateral, cephalic, and caudal views.

REMARKS.—This species is closely related to *B. indicus*, from which it differs by its distinctive coloration.

*Balbillus indicus*, n. sp.
Figs. 6–17

Uniformly pale yellow. Apex of clavus,

second and third apical cells of forewing suffused with brown.

Disc of vertex polished, medially, longitudinally grooved for 0.66 distance and ridged beyond. Forewing 2.5 times as long as wide, punctate along veins of corium, in cells of clavus, and along the costal margin, m-cu cross-veins two (as in *B. granulosus*) but not easily seen, fewer oblique veins reaching costal margin from outer anteapical cell.

MALE GENITALIA.—Pygofer simple, three times as long as its height with a few stout setae on caudoventral area, anal tube short. Plate parallel-sided, with single row of submarginal, stout, short setae, and hairlike setae along outer margin. Style without preapical lobe, apophysis long, its apex pointed and directed ventrad. Aedeagus with preatrium elongate, dorsal apodeme unpaired, short, shaft tubular for greater distance caudad, then flattened and deflected anteriorly, apex pointed; gonopore apical, large.

MEASUREMENTS.—Male 5.50 mm long, head 1.28 mm wide, pronotum 1.53 mm wide.

SPECIMEN EXAMINED.—Holotype ♂, India: Kerala: Thekkadi, 27.iii.1977, S. Viraktamath Coll. (UAS).

REMARKS.—In coloration and size it is similar to *B. albellus* Baker from the Philippines, but differs in forewing venation in having five apical cells rather than four as in the latter species.

## Genus *Stenotortor* Baker

*Stenotortor* Baker 1923a: 375, 377. Type species: *Stenotortor inocarpi* Baker, by original designation and monotypy.

Stucture similar to *Balbillus* but differs in the following respects. Orange with brick red or reddish brown markings. Median carina of vertex more prominent. Forewing without appendix, with one m-cu cross-vein, both anteapical cells open behind. Hind femoral spinulation 2+0+0. Hind tibial spinulation $R_1$ 20, $R_2$ 13, $R_3$ 10. Apex of hind basitarsus with three platellae.

Male pygofer simple, its caudoventral area thickly setose. Anal tube short. Male plate parallel-sided without macrosetae or long, hairlike setae. Style with well-developed, preapical lobe. Connective triangular, articulated with simple aedeagus. Gonopore large on ventral margin.

REMARKS.—Baker (1923a) differentiated *Stenotortor* from *Balbillus* by its strongly depressed body, tectiform tegmina with expanded costal area, strongly curved outer margin, and obscure venation. However, more important differences in *Stenotortor* appear to be the absence of an appendix on the forewing, the presence of one m-cu cross-vein, and hind femoral spinulation that is 2+0+0.

### *Stenotortor subhimalaya*, n. sp.

Figs. 18–27

Orange yellow. Vertex with oblique band on either side of median line, oblique line laterally; pronotum with lateral, oblique band, transverse band on scutellum dark reddish brown. Forewing with submarginal band on costal area, a stripe on clavus along commissure at basal 0.33 and then obliquely extending to inner claval margin, a median stripe connecting both claval stripe basally and inward extension of submarginal stripe both medially and caudally, dark reddish brown.

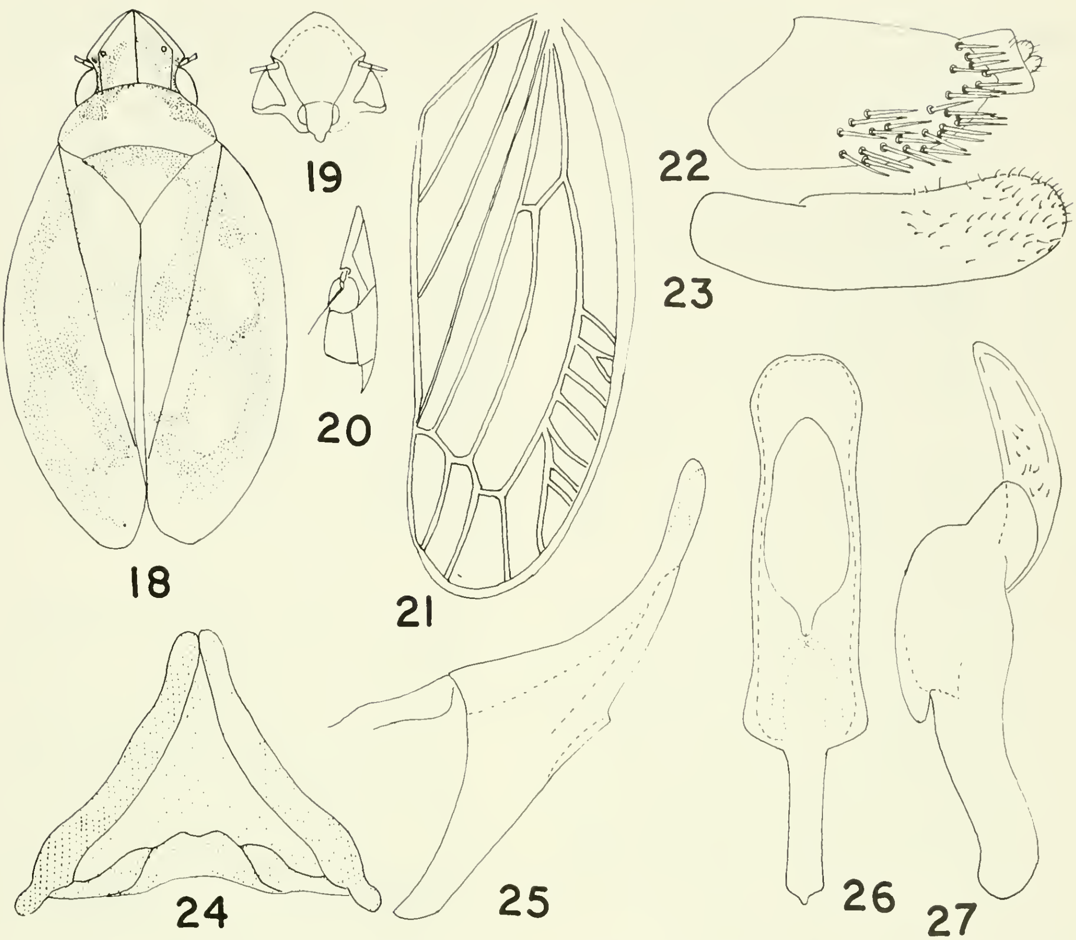
Vertex bluntly conical, slightly longer than its width between eyes. Face about as wide as long. Clypellus strongly narrowed apically. Lateral margin of pronotum strongly diverging, 2.7 times as wide as its median length. Forewing 2.4 times as long as its width. Hindwing with four apical cells.

MALE GENITALIA.—Pygofer twice as long as height, caudoventral margin with short, stout setae. Anal tube short. Male plate parallel-sided, about four times as long as wide, caudal apex rounded. Style with well-developed, stout, preapical lobe, apophysis fingerlike. Connective triangular. Aedeagus with elongate preatrium, without dorsal apodeme, shaft tubular in basal 0.33, then spatulate with large gonopore on its ventral margin occupying 0.66 of its length.

MEASUREMENTS.—Male 4.90 mm long; head 1.18 mm wide, pronotum 1.55 mm wide.

SPECIMENS EXAMINED.—Holotype ♂, India: West Bengal: Sukna, 3.xi.1981, C. A. Viraktamath Coll. no. 277 (UAS).

REMARKS.—This species differs from *S. inocarpi* in coloration of the vertex, pronotum, and wing pattern, in its larger size, and in its relatively longer aedeagus.




Figs. 18–27. *Stenotortor subhimalaya*, n. sp.: 18, habitus; 19, face; 20, head and thorax, profile; 21, forewing; 22, pygofer; 23, male plate; 24, connective; 25,26, aedeagus, lateral and caudal views; 27, style.

## Tribe Nirvanini

Pale yellow with dark or red markings. Body long, narrow, more or less depressed. Head as long as or longer than its width, disc of vertex longitudinally rugose in anterior region. Ocelli near lateral margins in front of eyes. Face with anterior, median carina and usually with lateral, oblique ridges on frontoclypeus. Gena narrow, lora small. Antennal pits rather deep, near anterior margin of eyes not visible from above; antennae long, reaching at least hind margin of pronotum. Forewings narrow, with reduced appendix and venation indistinct basally, second apical cell not widened apically. Hindwing with three or four apical cells. Fore and middle tibiae rounded. Hind femoral spinulation 2+1+1. Hind basitarsus terminated by two platellae.

Pygofer with well-developed, lateral lobes. Anal tube elongate, often with apical or caudoventral process. Male plate elongate, lonlonger than pygofer and apically rounded. Style variable, usually with slender apophysis that is curved, hooked, or avicephaliform. Connective free, Y-shaped. Aedeagus weakly sclerotized, usually with appendages.

REMARKS.—This group is most abundant among Nirvaninae and appears highly evolved compared to other tribes, considering the reduced wing venation, the more streamlined body form, and the specialized male genitalia.

Key to Genera of Nirvanini

1. Hindwing with four apical cells (Fig. 59) ....... 2
— Hindwing with three apical cells (Fig. 100) .... 3

2(1). Most parts of head, pronotum, and scutellum black dorsally; frontoclypeus and clypellus tumid (Figs. 85, 86); male connective rather T-shaped (Fig. 95) ............. *Chudania* Distant
— Dorsum of head, pronotum, and scutellum at most with black, narrow stripe terminated by round spot (Figs. 50, 60); frontoclypeus and clypellus flat (Figs. 29, 45, 49); male connective Y-shaped (Figs. 32, 75) ........... *Kana* Distant

3(1). Crown of head depressed in middle, margined by carina around its margin (Figs. 268, 269); male plate with angulate projection on its lateral margin near apex (Fig. 272); male style short, stout, appearing like loosely closed fist (Fig. 273) ........................... *Ophiuchus* Distant
— Crown of head either flat or convex; male plate either smoothly rounded near apex or with spine; style variable (Figs. 111, 148, 160, 182), slender and with slender apophysis that is curved, hooked, or avicephaliform ........... 4

4(3). Dorsal apodeme of aedeagus robust, bearing processes at least at base of shaft (Figs. 118, 139, 150, 171, 180, 206); male plate about four times as long as its width at its midlength (Figs. 114, 149, 170, 196); frontoclypeus with prominent, lateral ridges ................ *Sophonia* Walker
— Dorsal apodeme of aedeagus slender, U-shaped, without prominent processes (Figs. 225, 240, 254, 267); male plate five times or more as long as its width at its midlength (Figs. 227, 264); frontoclypeus with weak, lateral ridges ..................... *Nirvana* Kirkaldy

## Genus *Kana* Distant

*Kana* Distant 1908g: 285. Type species: *Kana thoracica* Distant, by original designation.

Pale yellow, often with bright-colored patches and stripes. Crown slightly (less than 1.5 times) longer than its width. Ocelli placed laterad of submarginal carina. Frontoclypeus with anterior ridge, rather flattened, with lateral, very prominent, ridgelike folds. Clypellus large, broad at base. Lora small. Face slightly longer than wide between eyes. Second apical cell of forewing parallel-sided. Hindwing with four apical cells. Hind tibial spinulation $R_1$ 20, $R_2$ 12 ± 1, $R_3$ 23. Hind basitarsus with two platellae.

Pygofer rounded caudally, with one or two rows of submarginal macrosetae; ventral process robust at base, narrowed apically. Male plate elongate, narrow, with outer margin sinuate. Connective Y-shaped, with arms joining broadly; apophysis robust, short, with slender apical extension. Aedeagus partially sclerotized, often depressed, with lateral, lamellate margin, gonopore surrounded by membranous tube with or without process, dorsal apodeme reduced.

REMARKS.—Some species of *Kana*, especially *K. bispinosa* and *K. nigropicta*, resemble externally the species of *Sophonia*. The four closed apical cells in the hindwing, however, distinguish this genus from *Sophonia* and *Nirvana*. The aedeagus of *Kana* is characteristic in that it is bent in its apical half and bears appendages surrounding the gonopore; the second apical cell on the forewing is not narrowed apically as is the case in both *Sophonia* and *Nirvana*. *Kana* is closely related to *Yaoundea* Linnavuori and even may prove to be synonymous with it. Both genera are related to *Chudania*, from which they differ in having a flatter frontoclypeus.

Key to Species of *Kana*

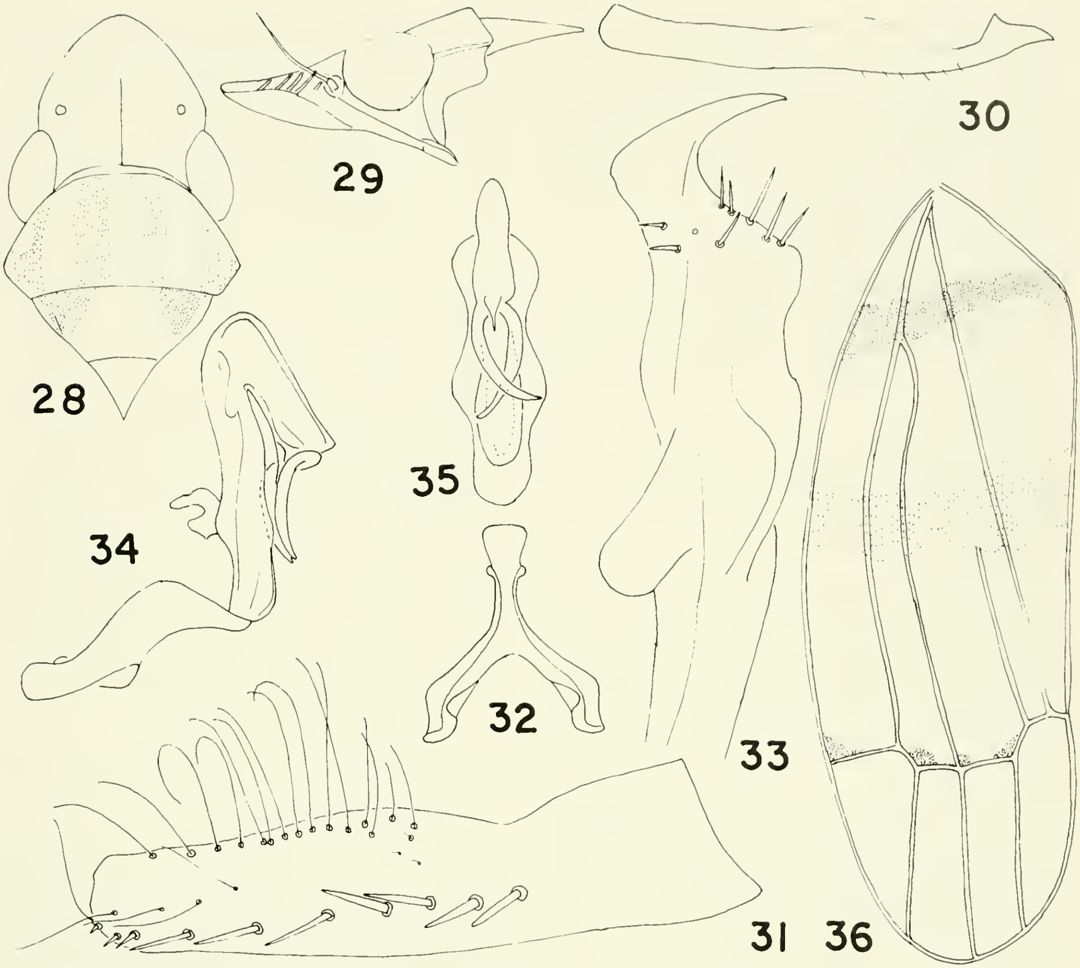
1. Vertex, pronotum, and scutellum traversed by a median, longitudinal, black line (Figs. 50, 60); third apical cell of forewing with large, round, black spot (Figs. 58, 61) .................... 2
— Vertex or pronotum or both either immaculate or with yellow, reddish, or orange stripes (Figs. 42, 44); forewing with brown or reddish orange, oblique, or transverse bands, black spot on third apical cell, if present very small (Figs. 36, 45, 47, 79) ...................................... 3

2(1). Vertex without black spot near apex (Fig. 50); aedeagal shaft with pair of pronglike processes (Fig. 55) ..................... *bispinosa*, n. sp.
— Vertex with black spot near apex (Fig. 60); aedeagal shaft without processes (Fig. 67) .... ........................... *nigropicta*, n. sp.

3(1). Forewing with transverse bands only (Figs. 36, 79) ...................................... 4
— Forewing with both oblique and transverse bands (Figs. 43, 47) ....................... 7

4(3). Forewing with single, broad, mottled brown, transverse band, area beyond apical cross-vein fuscous; vertex and pronotum marked with white stripes; male genitalia as in Figs. 74–78 ........................... *illaborata* Distant
— Forewing with two bands either both yellowish, orange, or red, or one orange red (more basal) and the other fuscous (median); apical cells at most with a few fuscous spots ................ 5

5(4). Pronotum without colored stripes; vertex with clear yellow, longitudinal stripe on each lateral side; forewing with two transverse, yellow fasciae ....................... *decora* (Melichar)
— Pronotum with orange stripes; vertex either immaculate or with orange-yellow, submarginal, apically converging stripes; forewing with basal, orange-yellow or red, and median, fuscous, transverse stripe ......................... 6




Figs. 28–36. *Kana ordinata* Distant: 28, head and thorax; 29, same, profile; 30, ventral pygofer process; 31, male plate; 32, connective; 33, style; 34, connective and aedeagus, lateral view; 35, aedeagus, caudal view; 36, forewing.

6(5). Vertex with pair of anteriorly converging, orange-yellow stripes continued on pronotum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *fasciata* Pruthi

— Vertex without stripes; pronotum with four orange stripes; male genitalia as in Figs. 30–35 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ordinata* Distant

7(3). Pronotum with two median, red stripes and two lateral, anterior, lemon yellow spots (Figs. 44); forewing with two red, transverse bands on corium (Fig. 47) . . . . . . . . . . . . . *thoracica* Distant

— Pronotum with anterior margin and two spots on posterior margin orange-yellow (Fig. 42); corium of forewing with three transverse, red bands (Fig. 43); male genitalia as in Figs. 37–41 . . . . . . . . . . . . . . . . . . . . . . . . . . *ramificata* Distant

## *Kana ordinata* Distant
Figs. 28–36

*Kana ordinata* Distant 1908g: 287. Lectotype ♂, Sri Lanka (BMNH, examined).

Yellow. Pronotum with two inner and two outer orange stripes joined posteriorly in male. Scutellum with brownish basal triangles. Forewing with reddish orange band across basal area, fuscous speckled band about midlength and series of fuscous spots at apices of anteapical cell.

Head slightly narrower than pronotum. Vertex of head slightly longer than its width between eyes (112:123), apex bluntly conical. Face with four prominent, lateral ridges.

MALE GENITALIA.—Pygofer rather squarish with caudodorsal area angulate, and with two rows of stout, long setae; ventral process with triangular, dorsal lobe and median, dorsal hump. Plate with rounded, caudal apex, with row of stout setae in caudal 0.66 and with

marginal row of long, hairlike setae. Style with well-developed, preapical lobe, apophysis short, stout, its apical extension slender, avicephaliform. Connective Y-shaped with stem as long as the length of arms. Aedeagus tubular with unsclerotized, poorly developed dorsal apodeme. Shaft strongly bent and directed ventrad and cephalad in apical 0.33, appearing rather like a compressed, inverted J, cephalic part of shaft laterally expanded and constricted in middle in cephalic view; caudal part with two long, curved processes that cross over and are longer than those in *K. ramificata*.

MEASUREMENTS.—Male body 3.00 mm long, forewing 4.10 mm long, head 1.17 mm wide, pronotum 1.25 mm wide. Female 6.40 mm long, head 1.30 mm wide, pronotum 1.32 mm wide.

SPECIMENS EXAMINED.—Lectotype ♂ labeled /Bogawantalawa, Ceylon, April/ /Distant Coll., 1911–383/ /1625/ /*Nirvana ordinata* Dist., type/ here designated (BMNH). Paralectotype ♀ labeled /Maskeliya, Ceylon, 8–05/ /Distant Coll., 1911–383/ here designated (BMNH).

REMARKS.—*Kana ordinata* is closely related to *K. ramificata* and differs in coloration and structure of the pygofer process. *Kana ordinata* has a shorter caudal part of the aedeagus and longer processes that cross over.

### *Kana ramificata* Distant
Figs. 37–43

*Kana ramificata* Distant 1908g: 286. Lectotype ♂, Sri Lanka (BMNH, examined).

Pale yellow, with submarginal band on vertex, anterior margin of pronotum and two spots on posterior margin orange. Scutellum golden yellow. Forewing with basal band connected by similar but more oblique band from costa to clavus and then continued on clavus but not reaching claval tip, orange; another oblique band with well-defined, orange, anterior margin and cross-veins limiting apical cells, reddish; spot at apex of clavus and another on third apical cell fuscous.

Head slightly narrower than pronotum (46:49). Vertex slightly longer than width between eyes, bluntly conical. Lateral ridges on face four in number, not prominent. Scutellum longer than pronotum.

MALE GENITALIA.—Pygofer rather squarish, with caudal tufts of long, stout setae; ventral process stout with dorsal, triangular process near caudal apex. Anal tube stout. Male plate with oblique row of stout setae in caudal 0.66, with long, hairlike setae, apex bluntly rounded. Style and connective as in *K. ordinata*. Aedeagus as in *K. ordinata*, but caudal bent part 0.66 as long as tubular cephalic part, apical processes shorter.

MEASUREMENTS.—Male 5.20 mm long, head 1.15 mm wide, pronotum 1.22 mm wide.

SPECIMEN EXAMINED.—Lectotype ♂ labeled /Green, Ceylon, 95–221/ /*Nirvana ramificata* Dist., type/ here designated (BMNH).

REMARKS.—*Kana ordinata* and *K. ramificata* share a similar basic pattern of male genitalia; however, they differ in the relative size of the aedeagal processes and the shape of the pygofer process. Both hindwings and the right side of the forewing of the lectotype are damaged and were placed in a microvial.

### *Kana thoracica* Distant
Figs. 44–48

*Kana thoracica* Distant 1908g: 285. Lectotype ♀, Sri Lanka (BMNH, examined).

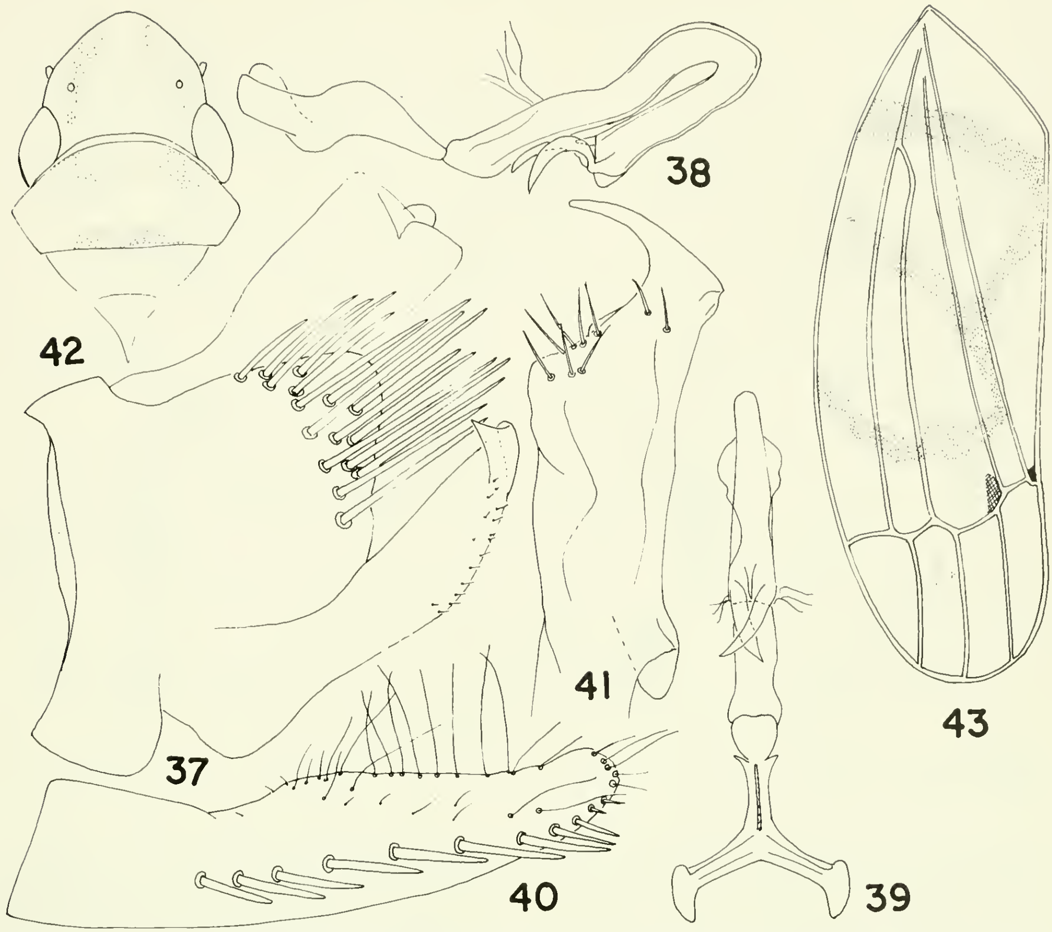
Pale yellow. Two anteriorly converging, submarginal stripes on vertex, two stripes one on either side of median line red, two lateral spots on anterior margin of pronotum lemon yellow. Forewing with red bands (Fig. 47) along anal margin, obliquely crossing over to clavus; short band on corium near base, another longer, oblique band about midlength from costal margin to clavus. Series of spots on either side of cross-veins separating apical cells fuscous.

Head narrower than pronotum (46:50). Vertex longer than its width between eyes (37:26). Face with three lateral, oblique ridges; longer than width including eyes. Pronotum shorter than both vertex (24:37) and scutellum (24:28).

FEMALE GENITALIA.—Hind margin of seventh sternum slightly concave with a median protuberance.

MEASUREMENTS.—Female 5.90 mm long, head 1.15 mm wide, pronotum 1.25 mm wide.

SPECIMEN EXAMINED.—Lectotype ♀ labeled /Pundaloya, Ceylon/ /Ceylon, Green




Figs. 37–43. *Kana ramificata* Distant: 37, male pygofer; 38, connective and aedeagus, lateral view; 39, same, caudal view; 40, male plate; 41, style; 42, head and thorax; 43, forewing.

Coll. 90–115/ /*Nirvana thoracica* Dist., type/ here designated (BMNH).

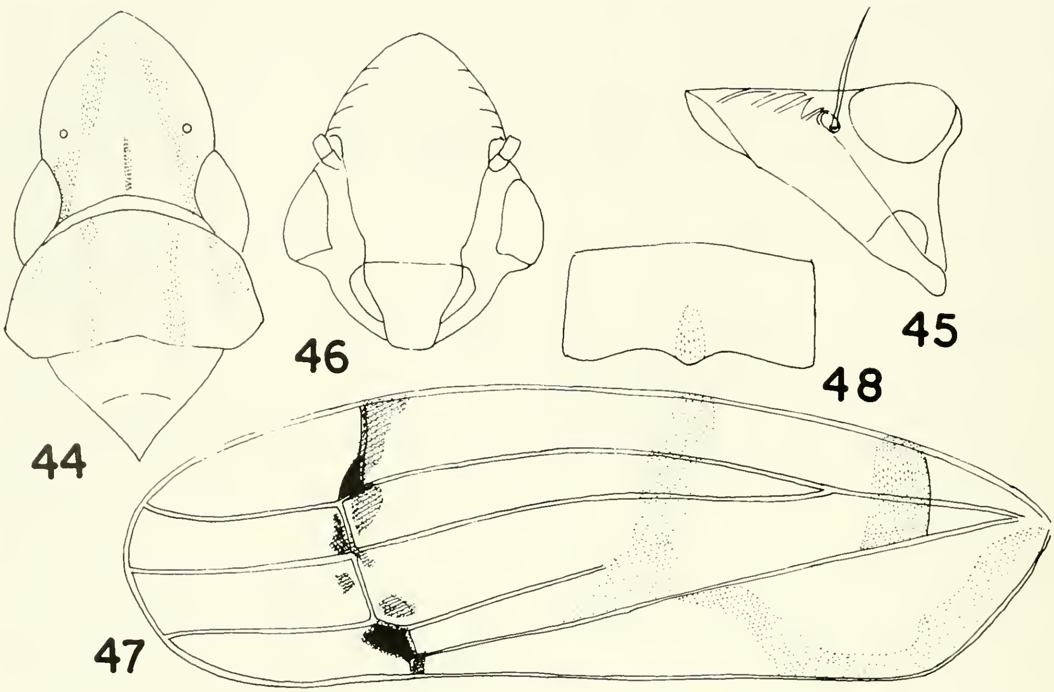
REMARKS.—This species appears to be related to *K. ramificata* and *K. ordinata*, from which it differs in coloration.

### *Kana bispinosa*, n. sp.
Figs. 49–59

Pale yellow. Vertex with median, longitudinal, black line from before apex and extending to the tip of scutellum, gradually widening posteriorly, lateral margin orange. Pronotum reddish. Forewings with suffused, red stripe adjoining thin, light brown stripe terminating on claval suture at 0.66 distance from base on anal margin, corium pinkish distally, claval apex and apical wing margin brown, third apical cell with large, black spot, surrounding area light brown, costal margin with three reddish fascia.

Head narrower than pronotum. Vertex slightly longer than width between eyes, flat, slightly depressed about center, apex bluntly conical, granulose. Apical half of face convex, basal half depressed, with three oblique ridges.

MALE GENITALIA.—Pygofer rounded, with stout, long setae along caudal margin; ventral process broad basally, abruptly narrowed and curved dorsally near apex. Male plate about four times as long as wide, distal 0.66 with an oblique row of stout spines and with marginal, hairlike setae. Style with stout, preapical lobe and short, stout apophysis, apical extension slender, beaklike. Connective Y-shaped with arms as long as stem. Aedeagus with short, well-developed preatrium; shaft with ridged




Figs. 44–48. *Kana thoracica* Distant: 44, head and thorax; 45, head, profile; 46, face; 47, forewing; 48, female seventh sternum.

lateral margins, somewhat rectangular, median ridge on caudal aspect running from base to apex, gonopore surrounded by membranous, tubelike structure bearing pair of ventrally directed, pronglike processes.

MEASUREMENTS.—Male 4.50 (4.50–4.60) mm long, head 0.93(0.90–0.95) mm wide, pronotum 0.99 (0.98–1.00) mm wide.

SPECIMENS EXAMINED.—Holotype ♂, India: Tamil Nadu: Naduvattam, 6.vi.1977, C. A. Viraktamath Coll. (UAS). Paratypes 2 ♂, data as in holotype but collected by S. Viraktamath (BMNH, UAS).

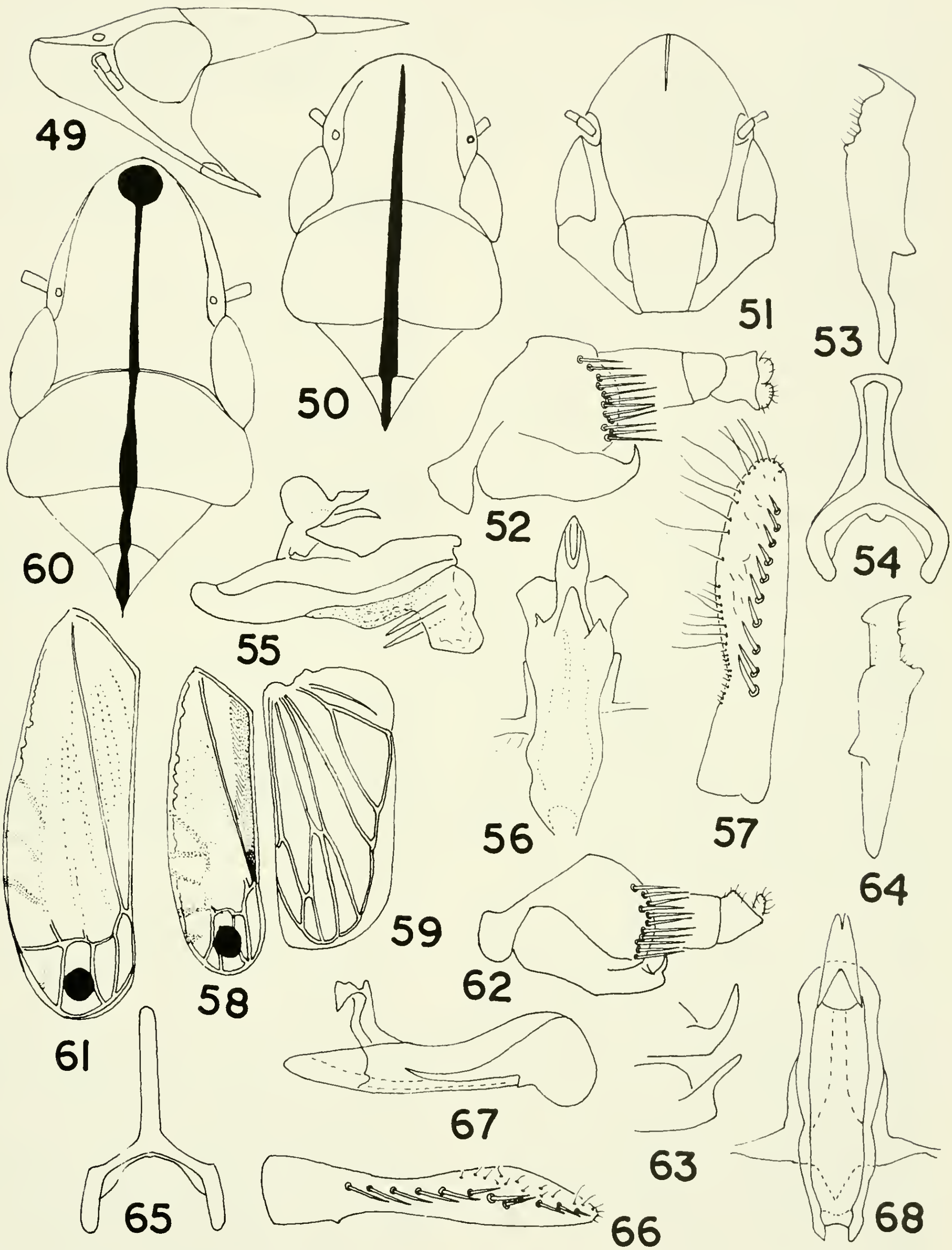
REMARKS.—This species is closely related to *Kana nigropicta* but only distantly related to *K. illaborata* and *K. ordinata*. It differs from the latter two species in coloration of the head, thorax, and forewing and in the structure of male genitalia.

*Kana nigropicta*, n. sp.
Figs. 60–68

Uniformly orange-yellow. Vertex with round, black spot near apex, contiguous with median, longitudinal, black line extending to tip of scutellum. Lateral margins of vertex and pronotum orange. Forewing with irregular, hyaline patches, claval apex brown, third apical cell with large, black spot, apical margin reddish, costal margin with three red, oblique fasciae, black spot in fourth apical cell.

Head as wide as pronotum. Vertex about 1.5 times as long as wide, anterior half convex, faintly granulose. Apical 0.25 of face slightly bulged with four lateral, oblique ridges. Pronotum transversely, finely rugulose. Scutellum longer than pronotum.

MALE GENITALIA.—Pygofer roundish with macrosetae along caudal margin; ventral process broad basally, abruptly narrowed near apex to mesally directed, pointed process. Anal tube moderately long. Male plate more than four times as long as wide, single row of macrosetae on caudal 0.75. Style with small, preapical lobe, apophysis stout with short, relatively stout apical extention. Connective Y-shaped with stem longer than arm. Aedeagus flattened, elongate with lateral, marginal, poorly sclerotized ridge, dorsal apodeme very short, gonopore large, on caudal margin, surrounded by membranous extension caudally.




Figs. 49–68. Species of *Kana: K. bispinosa*, n. sp.: 49, head and thorax, profile; 50, same, dorsal view; 51, face; 52, male pygofer; 53, style; 54, connective; 55, 56, aedeagus, lateral and ventral views; 57, male plate; 58, forewing; 59, hindwing. *K. nigropicta*, n. sp.: 60, head and thorax; 61, forewing; 62, male pygofer; 63, apex of ventral process of pygofer in two views; 64, style; 65, connective; 66, male plate; 67, 68, aedeagus, lateral and caudal views.

FEMALE GENITALIA.—Hind margin of seventh sternum almost straight. Ovipositor exceeding pygofers.

MEASUREMENTS.—Male 4.35 (4.20–4.50) mm long, head 0.92 (0.90–0.95) mm wide, pronotum 0.95 (0.90–0.95) mm wide. Female 5.13 (5.00–5.20) mm long, head 1.03 (1.00–1.08) mm wide, pronotum 1.11 (1.08–1.15) mm wide.

SPECIMENS EXAMINED.—Holotype ♂, India: Kerala: Thekkadi, 26.iii.1977, C. A. Viraktamath Coll. (UAS). Paratypes: 5 ♂, 2 ♀, data as in holotype but collected on 27.iii.1977 by C. A. Viraktamath (2 ♂, 1 ♀) (BMNH, USNM, UAS).

REMARKS.—This species can be easily recognized by the round, black spot on the vertex and the absence of processes on the membranous tube surrounding the gonopore.

### *Kana illaborata* Distant
Figs. 69–79

*Kana illaborata* Distant 1908g: 287. Lectotype ♂, Burma (BMNH, examined).

Yellow. Vertex with median, white stripe. Pronotum with narrow, median, irregular, lateral spot whitish. Forewing with broad, median, mottled, brown band on apical 0.33.

Head about as wide as pronotum (46:47). Vertex about as long as wide in male (29:28) but longer than its width in female (38:34). Pronotum shorter than both vertex and scutellum. Face with four lateral, oblique ridges and an apical, short, median ridge.

MALE GENITALIA.—Pygofer with lobelike, membranous process, armed with tooth mesally; caudal margin with series of hairlike setae. Male plate with oblique row of stout setae in caudal half, and with marginal, hairlike setae. Preapical lobe of style stout, apophysis relatively slender, apical extension slender. Connective Y-shaped, with stem as long as arm. Aedeagus laterally compressed, membranous for the most part, with pair of slender ventral processes and sclerotized tooth ventral to gonopore, which is elongate; pair of lamellate processes located in apical half of shaft.

MEASUREMENTS.—Male 5.70 mm long, head 1.15 mm wide, pronotum 1.17 mm wide. Female 6.30 mm long, vertex 1.37 mm wide, pronotum 1.42 mm wide.

SPECIMENS EXAMINED.—Lectotype ♂ labeled /Myitta (Doherty)/ /Distant Coll. 1911–383/ /*Kana illaborata* Dist., det. M. Webb, 1980/ here designated (BMNH). Paralectotype ♀ labeled /Tenass. Vall. Myitta (Doherty)/ /Distant Coll. 1911–383/*Nirvana illaborata* Dist. type/ here designated (BMNH).

REMARKS.—This species is very distinctive both in coloration and male genitalic characters and does not appear closely related to other species of *Kana*.

### *Kana decora* (Melichar)
Figs. 80–81

*Nirvana decora* Melichar 1903b: 166. Holotype ♀, Sri Lanka (ZMHU, examined).

The holotype female is a teneral specimen, and the diagnostic coloration is not very well developed. Melichar (1903b) has given a good description of this species and hence it is not redescribed here.

SPECIMEN EXAMINED.—Holotype ♀, labeled /Type/ /6178/ /Ceylon, nictus/ /*Nirvana*/ /*decora* m. det. Melichar/ /*Nirvana decora* Melichar/ (ZMHU).

### *Kana fasciata* Pruthi

*Kana fasciata* Pruthi 1930a: 22. Syntypes ♂, ♀, Sri Lanka (ZSI, not examined).

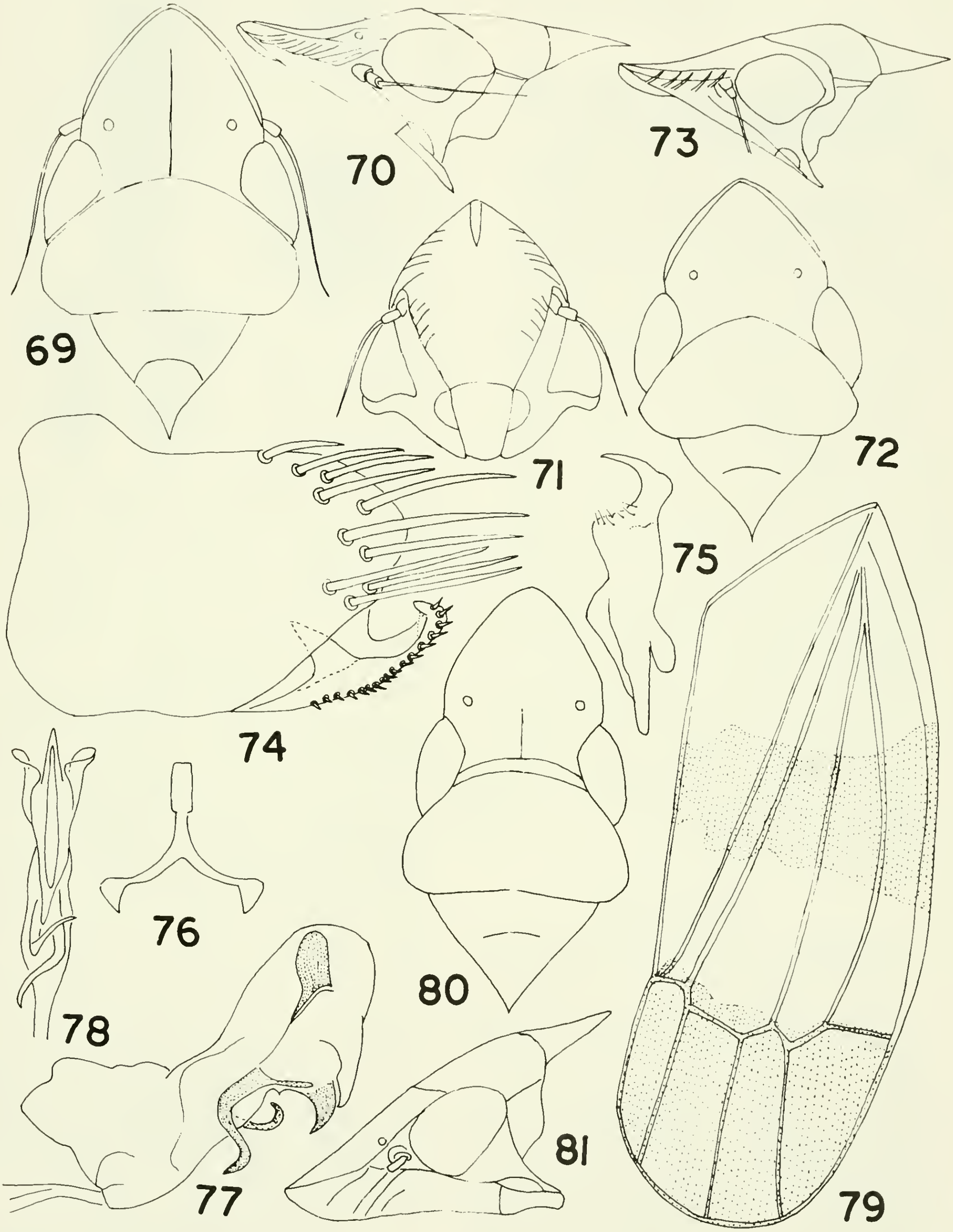
The types of this species were not available for study at the time the senior author visited ZSI. Pruthi's (1930a) description and illustrations suggest this to be a species with very distinctive coloration.

## Genus *Chudania* Distant

*Chudania* Distant 1908g: 268. Type species *Chudania delecta* Distant, by original designation and monotypy.

Yellow, with prominent broad stripe running on head, thorax, and along inner margin of clavus, extending laterally to occupy entire apex of forewing, black.

Vertex either as long as or slightly shorter than width, disc convex without median groove. Anterior area of disc rugose. Ocelli in front of and mesad of eyes. Frontoclypeus convex, with four to six transverse, prominent rugae evanescent medially on dorsal aspect and with median ridge in upper 0.75. Lora prominent. Clypellus large, slightly narrowed apically. Pronotum twice as wide as long, slightly longer than scutellum, polished and transversely, finely rugulose. Forewing with




Figs. 69–81. *Kana illaborata* Distant: 69, head and thorax, male; 70, same, profile; 71, same, face; 72, head and thorax, female; 73, same, profile; 74, male pygofer; 75, style; 76, connective; 77, 78, aedeagus, lateral and caudal views; 79, male forewing. *K. decora* (Melichar): 80, head and thorax; 81, same, profile.

appendix wanting, apical cells four and anteapical cells two. Hindwing with four apical cells. Hind tibial spinulation $R_1$ $18 \pm 2$, $R_2$ $12 \pm 1$, $R_3$ $12 \pm 1$.

Male pygofer with rounded, caudal margin, length shorter than height, strongly sclerotized with single, submarginal row of long setae and ventral process. Anal tube stout and large, about 0.8 times as high as height of pygofer. Male plate with uniseriate macrosetae in apical 0.66 and with long, hairlike setae. Style with prominent preapical lobe, apophysis slender, apex avicephaliform. Style rather T-shaped. Aedeagus membranous for most part, bent in midlength, laterally expanded, with ventrally directed, subapical, pronglike, sclerotized processes surrounding gonopore.

REMARKS.—This genus is related to *Kana* and *Afrokana* Heller with which it shares hindwing venation; with *Afrokana* it shares the structure of the male pygofer. However, they differ in the shape of the head. Linnavuori (1979) stated that *Afronirvana* Evans, *Chudania*, and *Afrokana* are very close, sharing, for instance, the same unique genital structure. He believes the recorded differences are too slight for separating them as valid genera. *Afrokana* is closer to *Kana* than to *Chudania* considering the peculiar shape of the aedeagus they share. It is likely that the study of more material of these genera, especially from Malaysia, Indonesia, and the Philippines, may prove that these taxa are congeneric with *Chudania*.

### *Chudania delecta* Distant
Figs. 82–96

*Chudania delecta* Distant 1908g: 268. Holotype ♀, India (BMNH, examined).

Male. Slender, darker than female. Vertex, pronotum, scutellum, upper part of face at level with lower margins of eyes, chocolate brown. Ocelli white, eyes dark brown. Forewing yellow, with posteriorly widening, black stripe along inner margin, occupying entire apical 0.33 of forewing (Fig. 82); two white, hyaline, triangular areas on costal area near apex and some cross-veins enclosing apical cells paler. Lower half of face, sterna, and legs yellow. Pygofer and fifth to eighth terga blackish.

Female. Similar to male but paler. Black markings of male, chocolate brown. Entire face, lateral margins of vertex in front of eyes, and pronotum yellow.

MALE GENITALIA.—Pygofer rounded caudally, with submarginal row of macrosetae, ventral process broad caudodorsally with finely serrated, dorsal margin. Male plate more or less of uniform width, caudally rounded, with outer, marginal, long, hairlike setae. Anal tube large, about as long as length of pygofer. Style with anterior part larger than posterior part to the point of articulation with connective. Stem of connective thrice as long as arms, apex expanded. Aedeagus membranous for most part, processes sclerotized, bent about its midlength, apical half robust, preatrium with short ventral and longer lateral processes; two pairs of processes arising where shaft bends, dorsal pair elongate, curved at midlength, the ventral pair shorter, three to five branched.

FEMALE GENITALIA.—Hind margin of seventh sternum straight. Ovipositor exceeding length of pygofer. Distal half of pygofer black.

MEASUREMENTS.—Male 4.62 (4.60–4.70) mm long, head 1.07 mm wide, pronotum 1.11 (1.07–1.12) mm wide. Female 5.38 (5.20–5.40) mm long, head 1.20 mm wide, pronotum 1.22 (1.20–1.25) mm wide.

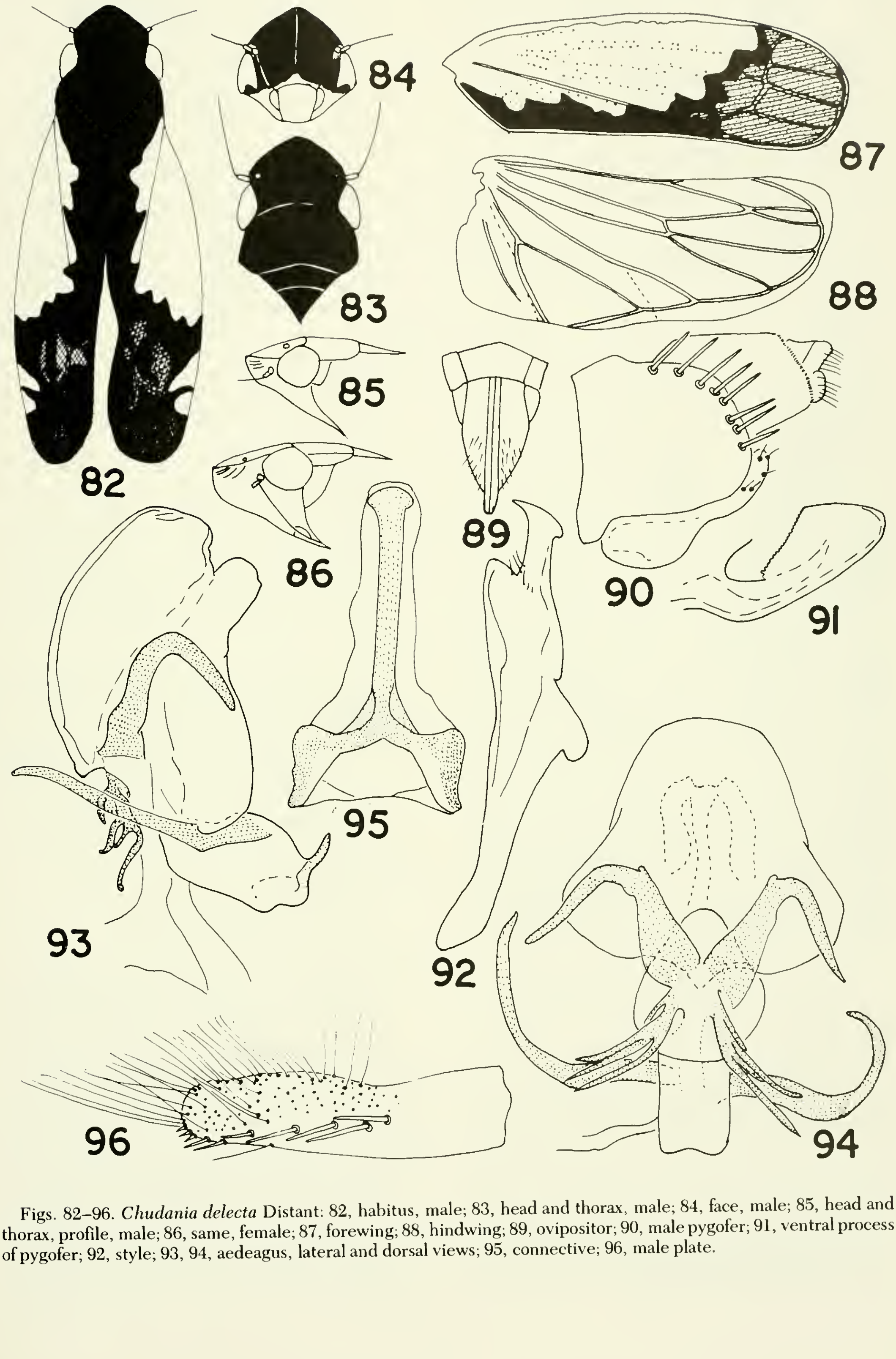
SPECIMENS EXAMINED.—Holotype ♀ labeled /Type, H.T./ /*Chudania delecta* Dist., type/ /Kurseong/ Distant Coll. 1911–383/ (BMNH). India: West Bengal: 8 ♂, 7 ♀, Kurseong, 1,483 m, 22.x.1981, C. A. & S. Viraktamath; 1 ♀, 15 km E Kalimpong, 1,780 m, 27.x.1981, C.A.V.; 4 ♂, 11 ♀, Kalimpong, 1,768 m, 29.x.1981, S.V.; 9 ♂, 19 ♀, 8 km E of Kalimpong, 1,968 m, 29.x.1981, C. A. V. Mizoram: 11 ♂, 11 ♀, Aizawl, 18.xi.1981, C. S. Wesley; 11 ♂, 14 ♀, Lungleh, 20–25.xi. 1981, C.S.W. (UAS).

REMARKS.—*Chudania delecta* and *C. africana* Heller are closely related but differ in coloration, shape of the ventral pygofer process, and the processes on the aedeagus. Also, the dorsal half of the aedeagus is more robust in *C. delecta* than in *C. africana*. The male genitalia of the third species, *C. exposita* Jacobi, is not known.

### Genus *Sophonia* Walker

*Sophonia* Walker 1870b: 327. Type species: *Sophonia rufitelum* Walker by monotypy.

*Pseudonirvana* Baker 1923a: 386. Type species: *Pseudonirvana sandakanensis* Baker, by original designation.




Figs. 82–96. *Chudania delecta* Distant: 82, habitus, male; 83, head and thorax, male; 84, face, male; 85, head and thorax, profile, male; 86, same, female; 87, forewing; 88, hindwing; 89, ovipositor; 90, male pygofer; 91, ventral process of pygofer; 92, style; 93, 94, aedeagus, lateral and dorsal views; 95, connective; 96, male plate.

*Quercinirvana* Ahmed & Mahmood 1970: 260. Type species: *Quercinirvana longicephala* Ahmed & Mahmood, by original designation. *New synonymy.*

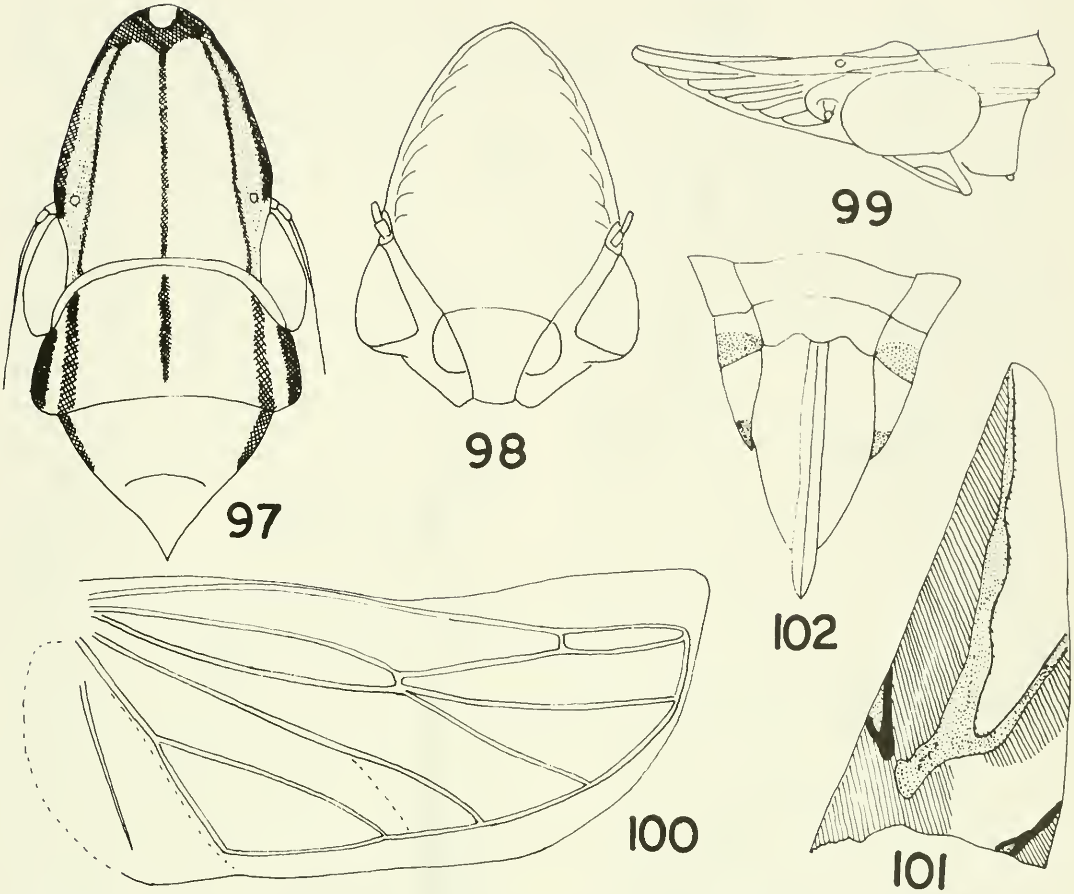
Head as wide as or wider than pronotum. Vertex as long as or longer than width between eyes, anterior half rugulose or granular, disc either flattened or slightly convex. Ocelli lateral in front of eyes. Frontoclypeus depressed, with prominent, lateral ridges and with median, apical ridge; face longer than width including eyes. Forewing with second apical cell narrowed apically. Hindwing with three apical cells. Hind tibial spinulation $R_1$ $20 \pm 2$, $R_2$ $12 \pm 1$, $R_3$ + 1, $R_4$ $18 \pm 2$.

Pygofer rounded or obtusely angled caudally, with or without caudal or ventral process; macrosetae confined to caudal 0.33 area. Anal tube prominent. Male plate broader than in *Nirvana*, three to four times as long as its width and rather parallel-sided with oblique row of stout spines in caudal 0.66 area and hairlike setae. Connective Y-shaped, its stem usually more than 1.5 times as long as each arm. Aedeagus with dorsal apodeme well developed, often with processes; preatrium variable, with or without processes; shaft tubular or lamellate, with or without process.

REMARKS.—Evans (1947a) suppressed *Pseudonirvana* as a junior synonym of *Sophonia*. This genus includes brightly colored species, often with red or orange streaks. It is closely related to *Kana* and *Nirvana*. It can be differentiated mainly by its shorter male plates and complex aedeagus that has processes on the dorsal apodeme and apex of the shaft. The holotype of *Sophonia rufitelum* is a female (Figs. 97–102). The relationships discussed here are based on species assigned to this genus from the Indian subcontinent.

Key to Species of *Sophonia*

1. Vertex as long as wide between eyes (Figs. 186, 198) .................................... 2
— Vertex longer than wide between eyes (Figs. 112, 208) .................................... 3
2(1). Male pygofer with long, ventral and short, dorsal process (Fig. 203); preatrium without processes ........................ *bifida*, n. sp.
— Male pygofer without processes; preatrium with a pair of processes (Fig. 191) .......... .......................... *modesta* (Distant)
3(1). Vertex and pronotum with either single or paired, black, longitudinal stripe(s) usually connected to black spot or spots near apex of vertex (Figs. 102, 112, 122) ................ 4
— Vertex and pronotum without black, median stripe or spot near apex; vertex sometimes with median, bright crimson streak (Figs. 164, 177) or orange stripe (Fig. 154) ................ 8
4(3). Vertex with two rather oval, contiguous spots, each connected to longitudinal, black line (Figs. 103, 104); aedeagal shaft bifid (Figs. 109, 110) ....................... *linealis* (Distant)
— Vertex with a large, round, black spot at apex either connected to or short distance away from one or paired longitudinal line(s) (Figs. 112, 122); aedeagal shaft not bifid .............. 5
5(4). Male pygofer without ventral or caudal process (Fig. 125); aedeagus as in Fig. 129; median, black lines on vertex not connected to its apical, round spot (Fig. 122) ................ ...................... *longitudinalis* (Distant)
— Male pygofer with ventral or caudal process; aedeagus variable but not as above (Figs. 118, 150); median, black stripe(s) of vertex connected to spot at apex (Figs. 112, 132) ........ 6
6(5). Vertex with single, median, black stripe (Fig. 142); male pygofer process short and narrow, apophysis of style hooklike; apex of each arm of dorsal apodeme with two long and short, median processes (Fig. 150) ........ *keralica*, n. sp.
— Vertex with two median, black stripes (Fig. 112); male pygofer process broad and long; apophysis of style beaklike; each arm of dorsal apodeme with a process on caudal margin (Fig. 118) .................................. 7
7(6). Male pygofer process with serrated, dorsal margin; process of dorsal apodeme exceeding width of shaft; shaft with pair of long, caudally directed processes (Fig. 118) ............. ............ *longicephala* (Ahmed & Mahmood)
— Male pygofer process not serrate apically; process of dorsal apodeme not exceeding width of shaft; processes of shaft short with basal, short, ventral tubercle (Figs. 139, 141) .. *bakeri*, n. sp.
8(3). Male pygofer without process; preatrium of aedeagus with process (Figs. 171, 180) ....... 9
— Male pygofer with process (Figs. 159, 214); preatrium of aedeagus without process ...... 10
9(8). Preatrium longer than broad in lateral aspect; longer process of dorsal apodeme not divided (Fig. 171); vertex with short, median, crimson streak in apical 0.66 but not reaching apex ... .......................... *insignis* (Distant)
— Preatrium broader than long, longer process of dorsal apodeme bifid (Fig. 180); vertex uniformly whitish yellow with median, crimson streak bifid near apex (Fig. 175) . *complexa*, n. sp.
10(8). Vertex with median, broad, orange stripe continued on pronotum, anteriorly narrowed; posterior half on pronotum broadened and blackish, scutellum blackish (Figs. 154, 155); pygofer process short, bladelike, and pointed at apex (Fig. 159); aedeagus shaft tubular with apical, ventrally directed, platelike process (Figs. 162, 163) ........... *illuminata* (Distant)




Figs. 97–102. *Sophonia rufitelum* Walker: 97, head and thorax; 98, face; 99, head and thorax, profile; 100, hindwing; 101, basal half of clavus; 102, ovipositor.

— Vertex, pronotum, and scutellum whitish yellow; pygofer process long, slender, and elbowed (Fig. 214); aedeagus not as above (Fig. 218) ...................... *complicata*, n. sp.

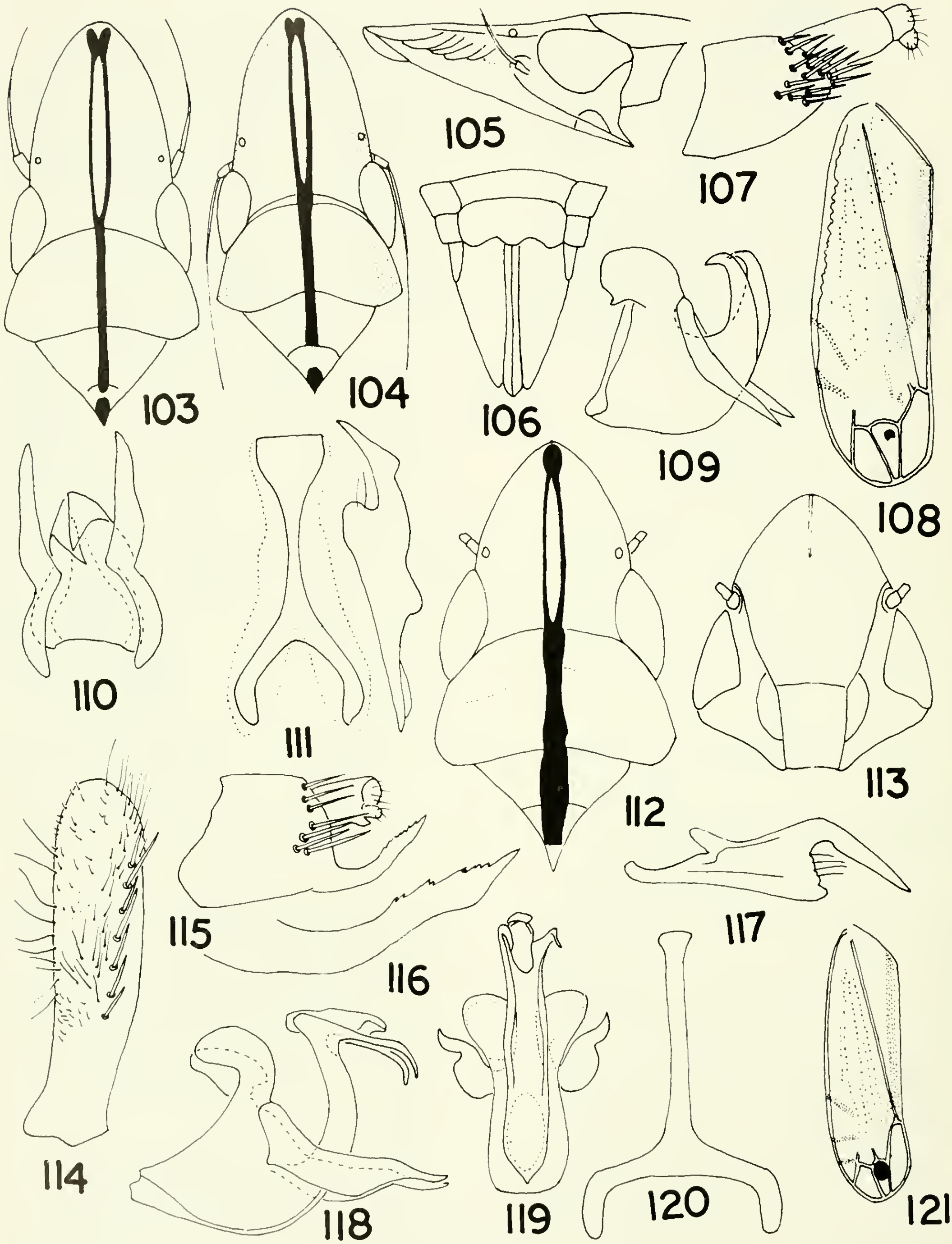
### *Sophonia linealis* (Distant)
Figs. 103–111

*Nirvana linealis* Distant 1908g: 282. Holotype ♀, India (BMNH, examined).
*Nirvana greeni* Distant 1908g: 283. Holotype ♀, Sri Lanka (BMNH, examined). *New synonymy.*

Yellow. Vertex with two piceous, apical, elongate, fused spots from which longitudinal, piceous lines traverse posteriorly meeting posterior margin of vertex, lateral margin often with orange-yellow stripe confined to ocelli or extending anteriorly. Pronotum and scutellum with median, longitudinal, piceous line often interrupted before apex of scutellum. Claval margin of forewing piceous with piceous stripe bent obliquely near claval apex and reaching claval suture; spot on second apical cell and two oblique lines from costa in apical half piceous.

Head about as wide as pronotum. Vertex more than 1.5 times as long as wide in male, nearly twice as long as wide in female, lateral margin raised. Scutellum longer than pronotum. Second apical cell of forewing narrowed apically.

MALE GENITALIA.—Pygofer ovate, without ventral process. Plate slightly more than 3.5 times as long as median width, slightly narrowed caudally. Style with broad, preapical lobe and beaklike extension of apophysis relatively short. Stem of connective flared caudally, about twice as long as each arm. Dorsal apodeme of aedeagus robust, each arm with caudally directed, elongate process that exceeds width of shaft; shaft tubular, curved, hooked apically where it appears bifid.




Figs. 103–121. *Sophonia linealis* (Distant): 103, head and thorax of holotype female *Nirvana greeni* Dist.; 104, head and thorax of holotype of *Nirvana linealis* Dist.; 105, profile; 106, ovipositor; 107, male pygofer; 108, forewing; 109, 110, aedeagus, lateral and dorsal views; 111, connective and style. *S. longicephala* (Ahmed & Mahmood): 112, head and thorax; 113, face; 114, male plate; 115, male pygofer; 116, ventral process of pygofer; 117, style; 118, 119, aedeagus, lateral and caudal views; 120, connective; 121, forewing.

FEMALE GENITALIA.—Hind margin of seventh sternum straight with median protuberance.

MEASUREMENTS.—Male 4.06 (4.00–4.10) mm long, head 0.83 (0.80–0.85) mm wide, pronotum 0.88 (0.85–0.93) mm wide. Female 4.82 (4.50–5.00) mm long, head 0.93 (0.88–0.95) mm wide, pronotum 0.98 (0.93–1.03) mm wide.

SPECIMENS EXAMINED.—Holotype ♀, labeled /Type, H.T.//Peradeniya, 2.08, Ceylon/ /Distant Coll. 1911–383/ /*Nirvana greeni* Dist., type/ (BMNH). Holotype ♀, labeled /Type, H.T./ /Calcutta, 6.6.07/ /Distant Coll. 1911–383/ /*Nirvana linealis* Dist., type/ (BMNH). India: Karnataka: 6 ♀, Dharwar, 26.iii.1972; 1 ♀ 29.iv.1969; 1 ♀, —.i.1970; 1 ♀, 14.iv.1972; 1 ♀, —.x.1979 C. A. Viraktamath Coll.; 3 ♂, 3 ♀, Chamarajanagar, 12.viii.1977; 4 ♀, Hunsur, 16.i.1978; 1 ♀, Bangalore, 11.vi.1977; 1 ♀, Arsikere, 23.vii.1978; 1 ♂, 1 ♀, 16.i.1979; 1 ♀, Sulikere, 30.xii.1976, all collected by C. A. Viraktamath (UAS). Kerala: 3 ♂, 6 ♀, Kayangulum, —.viii.1983, ex coconut (UAS).

REMARKS.—The holotypes of *linealis* and *greeni* show color differences, especially the extension of the median, dark fuscous stripe of the pronotum along the inner margin of the clavus in *greeni*, which is absent in *linealis*. The female seventh sterna are identical; hence the species are considered as synonyms. This species is unique among *Sophonia* in having a bifid aedeagal shaft.

### *Sophonia longicephala* (Ahmed & Mahmood), n. comb.

Figs. 112–121

*Quercinirvana longicephala* Ahmed & Mahmood 1970: 263. Holotype ♂, Pakistan (University of Karachi, not examined).

Pale yellow, elongate, black spot near apex of vertex contiguous with two longitudinal, black lines that fuse at base of vertex and continue as single line to near tip of scutellum. Forewing with broad, brown stripe along claval commissure reaching claval apex and obliquely crossing corium, apical margin suffused with brown, costal margin with anterior, oblique and two posterior, transverse, black fasciae; second apical cell with black spot.

Head nearly as wide as pronotum. Vertex about 0.33 times longer than wide, disc depressed, faintly granulose. Second apical cell narrowed caudally.

MALE GENITALIA.—Pygofer trapezoidal, with long, caudally directed ventral process dorsally serrated. Plate about four times as long as wide, distal 0.66 with a single row of macrosetae and hairlike setae. Style with large, preapical lobe, beaklike extension of apophysis long. Aedeagus with dorsal apodeme well-developed, caudally directed, apically pointed processes that exceed width of shaft, shaft tubular, dorsoanteriorly curved with subapical, caudally directed, slender, elongate processes.

MEASUREMENTS.—Male 4.50 (4.30–4.70) mm long, head 0.91 (0.90–0.93) mm wide, pronotum 0.96 (0.93–1.00) mm wide.

SPECIMENS EXAMINED.—India: Haryana: 1 ♂, Kalka, 29.i.1979, C. A. Viraktamath; Himachal Pradesh: 1 ♂, Kulu, 1.iv.1978, I. Dworakowska (UAS).

REMARKS.—This species is related to and resembles externally *S. bakeri*. The spot on the vertex in this species is rather oval (as in *bakeri*), and it differs in the details of the male pygofer process and the aedeagus.

### *Sophonia longitudinalis* (Distant)

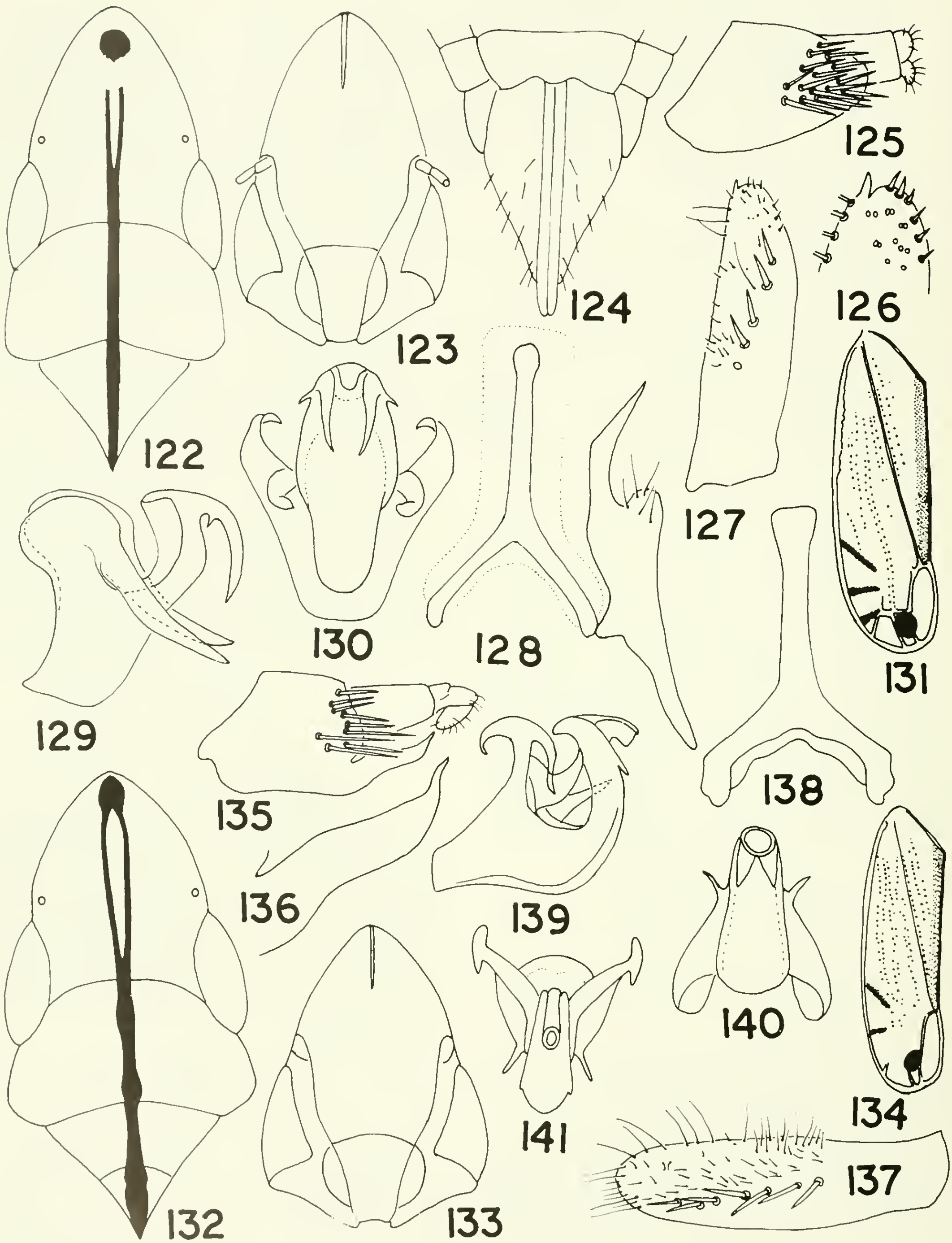
Figs. 122–131

*Nirvana longitudinalis* Distant 1908g: 283. Lectotype ♀, Burma (BMNH, examined).

Vertex pale yellow with large, subapical, black spot and two median, longitudinal lines, not reaching black spot and fused near hind margin of vertex, continued on pronotum and scutellum as median stripe and on clavus as irregular stripe. Forewing with large, round, black spot in second apical cell extending partly to first apical cell, apical margin suffused with brown.

Head as wide as pronotum or slightly narrower. Vertex about 1.5 times as long as wide, apex subangular, disc mildly convex, granulose. Second apical cell narrowed caudally.

MALE GENITALIA.—Pygofer ovate, ventral process wanting, macrosetae limited to distal 0.33. Plate about 3.5 times as long as width, with short tooth at the outer apical margin. Style with short, preapical lobe, apophysis with long, beaklike extension. Aedeagus with robust, dorsal apodeme, each of its arms bearing an elongate, caudally directed process, preatrium wanting, shaft lamellate with lateral margin caudally curved, widest at apical




Figs. 122–141. *Sophonia longitudinalis* (Distant): 122, head and thorax; 123, face; 124, ovipositor; 125, male pygofer; 126, 127, male plate; 128, connective and style; 129, 130, aedeagus, lateral and caudal views; 131, forewing. *S. bakeri*, n. sp.: 132, head and thorax; 133, face; 134, forewing; 135, male pygofer; 136, pygofer process; 137, male plate; 138, connective; 139–141, aedeagus, lateral, caudal, and dorsal views.

half with long, slender, arcuate, apically pointed, ventrally curved process that bears a short tooth on its outer margin at base.

FEMALE GENITALIA.—Hind margin of seventh sternum slightly concave. Ovipositor slightly exceeding pygofer.

MEASUREMENTS.—Male 4.43 (3.80–5.40) mm long, head 0.96 (0.80–1.43) mm wide, pronotum 0.96 (0.85–1.13) mm wide. Female 4.90 (4.60–5.30) mm long, head 1.02 (0.98–1.10) mm wide, pronotum 1.05 (1.00–1.10) mm wide.

SPECIMENS EXAMINED.—Lectotype ♀ labeled /Myitta (Doherty)/ /Distant Coll. 1911–383/ /*Nirvana longitudinalis* Dist., type/ here designated (BMNH). India: Karnataka: 6 ♂, Mudigere, 4–6.iv.1980, C. A. Viraktamath; 1 ♀, 7.iv.1975, C.A.V.; 1 ♀, Kodlipet, 6.iv.1975; 1 ♂, Hunsur, 10.i.1978; 1 ♀, Bannerghatta, 12.ix.1976, B. Mallik; Kerala: 1 ♀, Thekkadi, 27.iii.1977, C.A.V. Nepal: Nagarkot, 1 ♂, 1 ♀, 15.ix.1979; I. Dworakowska (UAS). Burma: 1 ♀, Amberst Dist., Kawkareik, 19–20.xi.1911, F.H.G. (ZSI).

REMARKS.—This species can be distinguished from all other species of *Sophonia* by its lamellate aedeagal shaft and tooth on the apex of the male plate.

## *Sophonia bakeri*, n. sp.

Figs. 132–141

Pale yellow to whitish yellow. Vertex with black spot near apex, joined by two black, longitudinal lines that fuse basally and extend to scutellum. Pronotum and scutellum sometimes with reddish spots, scutellum in male entirely reddish. Forewing with brown stripe close to or along anal margin, marked with yellow along inner margin, apex of clavus and apical margin brown, costal margin with anterior, oblique and posterior, transverse, brown fasciae, second apical cell with large, black spot.

Vertex about 1.5 times as long as wide, apex subtriangular, disc depressed. Posterior half of pronotum transversely rugulose. Second apical cell narrowed at apex.

MALE GENITALIA.—Pygofer with ventrocaudal angle produced to process with attenuated apex. Plate 3.5 times as long as wide. Apophysis of style with long, beaklike extension. Stem of connective 1.5 times as long as each arm. Aedeagus with each arm of dorsal apodeme robust, bearing triangular process on caudal margin; preatrium short; shaft tubular, caudodorsally curved, apex strongly incurved with ventrally directed, short, pronglike process on caudal margin subapically.

FEMALE GENITALIA.—Hind margin of seventh sternum concavely emarginate. Ovipositor exceeding length of pygofer.

MEASUREMENTS.—Male 4.48 (4.30–5.00) mm long, head 0.90 (0.85–1.00) mm wide, pronotum 0.88 (0.78–1.03) mm wide. Female 5.08 (4.70–5.30) mm long, head 1.04 (0.93–1.23) mm wide, pronotum 1.05 (1.00–1.10) mm wide.

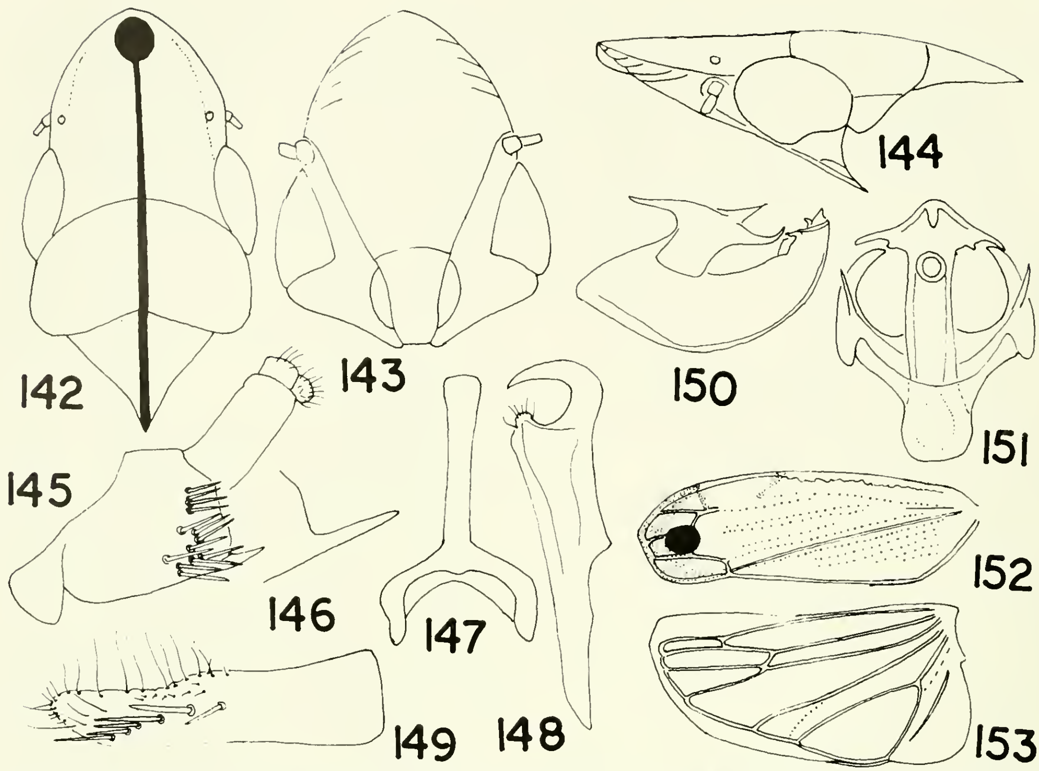
SPECIMENS EXAMINED.—Holotype ♂, India: Karnataka: Mudigere, at light, 4–6.iv.1980, C. A. Viraktamath (UAS). Paratypes: India: Karnataka: 2 ♂, Dharwar, —.i.1970, C. A. Viraktamath; 1 ♀, Kodlipet, 6.iv.1975, C.A.V.; 1 ♀, Bangalore, 9.iii.1975, C.A.V.; 1 ♀, Kalhalla, 18.i.1978, C.A.V., 1 ♀, Mudigere, 23.ix.1973, C.A.V.; 1 ♂, 1 ♀, Kemmanagundi, 8.iv.1975, K. D. Ghorpade; Kerala: 1 ♂, Thekkadi, 27.iii.1977, S. Viraktamath; Maharashtra: 1 ♀, Matheran, 915 m, 23.xi.1977, C.A.V.; Tamil Nadu: 1 ♂, Kodaikanal, 2,250 m, 10.vi.1980, C. S. Wesley; Uttar Pradesh: 1 ♂, 1 ♀, Dehra Dun, 28.iv.1975, C.A.V.; Nepal: 2 ♀, Gokarna, 14.ix.1979, I. Dworakowska; 1 ♀, Sarankot, 17.ix.1979, ex *Quercus* sp., I.D. (1 ♂ and 1 ♀ in BMNH, IARI, USNM, and rest in UAS).

REMARKS.—*Sophonia bakeri* is related to *S. longitudinalis* and *S. longicephala* as they share similar external coloration and male genitalia. They form a closely knit group. *S. bakeri* differs from the other two by its shorter process of the dorsal apodeme and aedeagal process.

## *Sophonia keralica*, n. sp.

Figs. 142–153

Uniformly yellow. Vertex with round, black spot near apex connected by single, median, longitudinal, black line, discontinuous for short distance near black spot and then continued to apex of scutellum. Lateral margin of vertex orange basally. Forewing with claval suture and punctures along cubital vein brown, second and part of third apical cells occupied by large, black spot; costal margin with anterior, oblique and posterior, transverse, black fasciae, apex of clavus and apical margin brownish.




Figs. 142–153. *Sophonia keralica*, n. sp.: 142, head and thorax; 143, face; 144, head and thorax, profile; 145, male pygofer; 146, pygofer process; 147, connective; 148, style; 149, male plate; 150, 151, aedeagus, lateral and cephalic views; 152, forewing; 153, hindwing.

Head nearly as wide as pronotum. Vertex slightly longer than wide, disc flat, depressed near apex. Scutellum slightly longer than pronotum. Second apical cell of forewing narrowed slightly near apex.

MALE GENITALIA.—Pygofer caudally rounded, its ventrocaudal angle produced to sharp, thin process, five macrosetae along caudal margin in straight line, black, rest hyaline. Anal tube as long as pygofer. Plate four times as long as wide. Style with strongly hooked apophysis. Stem of connective 1.5 times as long as each arm. Dorsal apodeme of aedeagus slender, each arm with ventral, dorsal, and short, median process; shaft tubular with pair of laterally directed processes, gonopore subapical.

MEASUREMENTS.—Male 3.90 mm long, head 0.90 mm wide, pronotum 0.93 mm wide.

SPECIMEN EXAMINED.—Holotype ♂, India: Kerala: Thekkadi, 27.iii.1977, S. Viraktamath Coll. (UAS).

REMARKS.—*Sophonia keralica* is related to *S. illuminata*. Both have similar male genitalia. They differ, however, in coloration and detailed structure of the aedeagus.

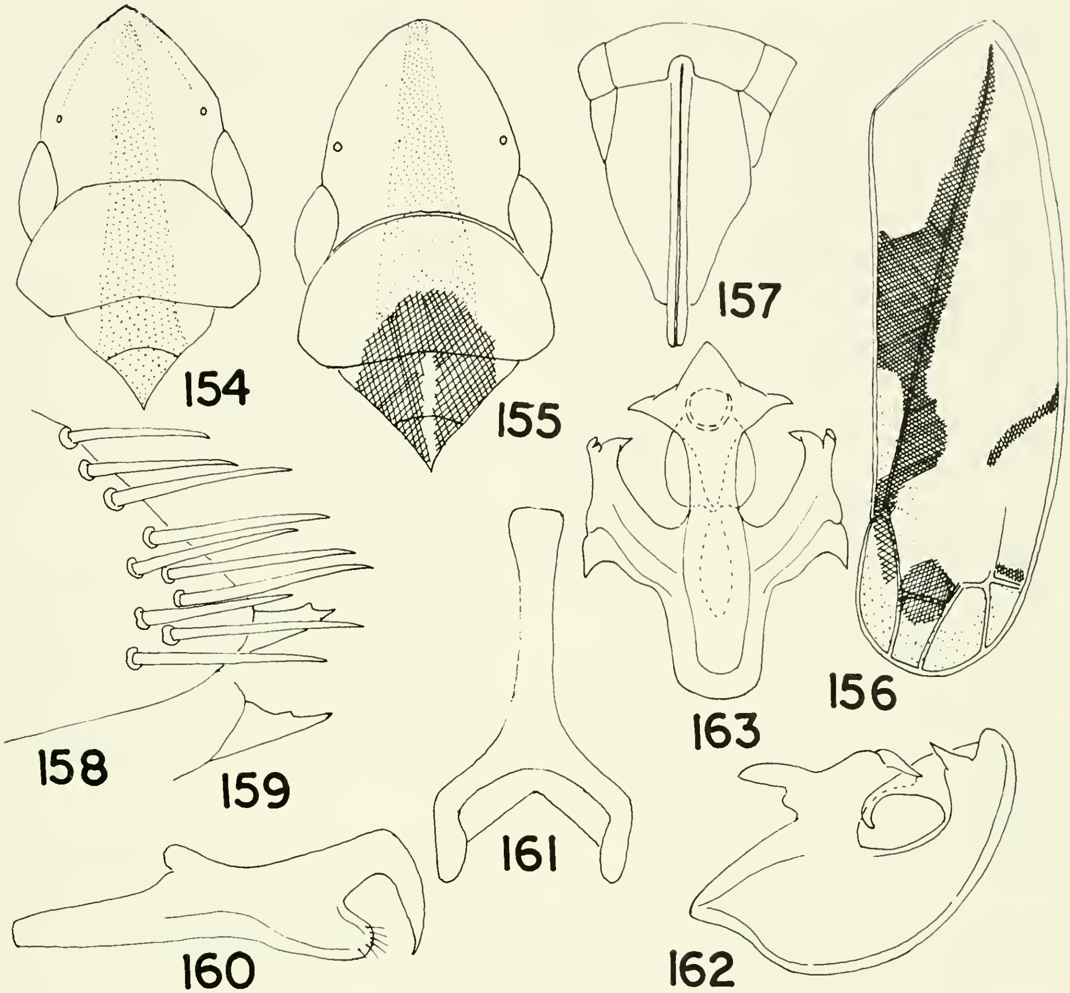
## *Sophonia illuminata* (Distant), n. comb.

Figs. 154–163

*Kana illuminata* Distant 1918b: 35. Lectotype ♂, India (BMNH, examined).

*Kana signata* Distant 1918b: 34. Lectotype ♀, India (BMNH, examined). *New synonymy.*

Female. Vertex and pronotum creamy white with yellowish lateral areas, median stripe narrowing to apex of vertex sanguineous on vertex and anterior half of pronotum, widened in posterior half where it is black. Scutellum black except for two lateral, basal spots. Clavus along claval suture and apical half piceous except for subapical, elongate, orange spot. Corium along its inner margin piceous which widens near apex of clavus and changes to orange; appendix fuscous, two large, round spots in second apical cell,




Figs. 154–163. *Sophonia illuminata* (Distant): 154, head and thorax of lectotype male *Kana illuminata;* 155, head and thorax of lectotype female *Kana signata* Distant; 156, forewing, female; 157, ovipositor; 158, apex of male pygofer; 159, pygofer process; 160, style; 161, connective; 162, 163, aedeagus, lateral and caudal views.

oblique line at apical 0.33 of costa and more distal, transverse band piceous, rest of wing yellow and areas anterior to piceous spots whitish.

Male. Coloration less extensive compared to female. Stripe on vertex continuing on pronotum and scutellum, gradually widening and sanguineous throughout. Forewing coloration comparatively less developed.

Head narrower than pronotum, median length of vertex slightly longer than width between eyes. Face longer than wide.

MALE GENITALIA.—Pygofer lobe gradually narrowed caudally and terminated by sharp, triangular process and with series of stout, long spines. Plate parallel-sided, with six stout setae in oblique row commencing at midlength, third to fifth setae black in color. Style with stout, preapical lobe and hooklike, rather slender apophysis with attenuated apex. Connective with stem 1.5 times as long as each arm. Aedeagus with short, dorsal pair of blunt processes and ventral, fingerlike process; shaft robust at base, narrowed apically with dorsal, large gonopore surrounded by two lateral, pronglike processes and ventrally directed, lobelike plate.

FEMALE GENITALIA.—Hind margin of seventh sternum concave. Ovipositor exceeding length of pygofer.

MEASUREMENTS.—Male 4.40 mm long, head 1.00 mm wide, pronotum 1.05 mm wide. Female 5.1 mm long, head 1.12 mm wide, pronotum 1.12 mm wide.

SPECIMENS EXAMINED.—3 syntype ♂ of *Kana illuminata* mounted on single card labeled /S. India, Madras, Kodaikanal, T. V. Campbell, K.K.4.16/. One of these was removed, remounted, and relabeled by the senior author, /Kodaikanal, S. India, T. V. Campbell/ and is here designated as lectotype; others designated paralectotypes. One paralectotype ♂ labeled /Kodaikanal, India, T. V. Campbell/ /S. India, E. A. Butler, 1915–60/ /*Kana illuminata* Dist., type/ (BMNH). Lectotype ♀ labeled /Kodaikanal, S. India, T. V. Campbell, K.K.5.11/ /S. India, E. A. Butler, 1915–60/ /54,9/ /*Kana signata* Dist., type/ here designated (BMNH). India: Tamil Nadu: 1 ♀, Trichinopoly, J. Dubrenil (IRSNB); 1 ♀ Kadaikanal, 2,030–2,150 m, —.viii.1922, S. Kemp (ZSI).

REMARKS.—*Sophonia illuminata* and *S. signata* are the male and female, respectively, of the same species based on the similarity in external coloration and structure. This species is closely related to *S. keralica*. Both have a similar type of male genitalia but differ in coloration and structure of the pygofer process and aedeagus.

### *Sophonia insignis* (Distant), n. comb.

Figs. 164–174

*Nirvana insignis* Distant 1918b: 33. Lectotype ♂, India (BMNH, examined).

Whitish yellow. Median groove on vertex crimson from about center to just short of apex, lateral marginal area orange. Forewing hyaline, light brown stripe along anal margin rarely reaching apex of clavus, if so occupying entire quarter of clavus, or stripe wanting, apex of clavus brown; costal margin with two long, oblique fasciae, third transverse and fourth short, broad, oblique fasciae in the distal half brown; apical margin brown; second apical cell with black spot.

Head narrower than pronotum. Vertex about 1.5 times as long as wide between eyes; disc flat or slightly depressed toward base, apex granulose. Second apical cell of forewing slightly narrowed distally.

MALE GENITALIA.—Caudal lobe of pygofer rounded, without processes. Plate about 3.5 times as long as wide. Preapical lobe of style robust, apophysis slender, with apical extension forming short, beaklike extension. Aedeagus with preatrium well developed, with ventrocaudally directed process, about as long as preatrium; dorsal apodeme broad, platelike, with two processes (one short, pronglike on cephalic margin, other long, slender, and inwardly curved in middle) and ventral, short process; shaft tubular, curved anteriorly then ventrally near apex.

FEMALE GENITALIA.—Hind margin of seventh sternum straight. Ovipositor slightly extending beyond pygofer.

MEASUREMENTS.—Male 5.00 (4.80–5.20) mm long, head 0.97 (0.93–1.00) mm wide, pronotum 1.04 (1.03–1.07) mm wide. Female 5.62 (5.00–6.10) mm long, head 1.06 (0.98–1.13) mm wide, pronotum 1.14 (1.03–1.23) mm wide.

SPECIMENS EXAMINED.—Lectotype ♂ labeled /Tenmalai, W. Ghat (W. side). Travancore, 22.xi.08, Annandale/ /Distant Coll. 1911–383/ here designated (BMNH). Paralectotype ♀, with same data as in holotype, here designated (ZSI). India: Kerala: 11 ♂, 6 ♀, Thekkadi, 26–27.iii.1977, C. A. Viraktamath, S. Viraktamath, and B. Mallik Coll.; Karnataka: 2 ♀, Mudigere, 7.iv.1980, C.A.V. (UAS).

REMARKS.—This species is closely related to *S. complexa* and can be differentiated by the structure of male genitalia and coloration.

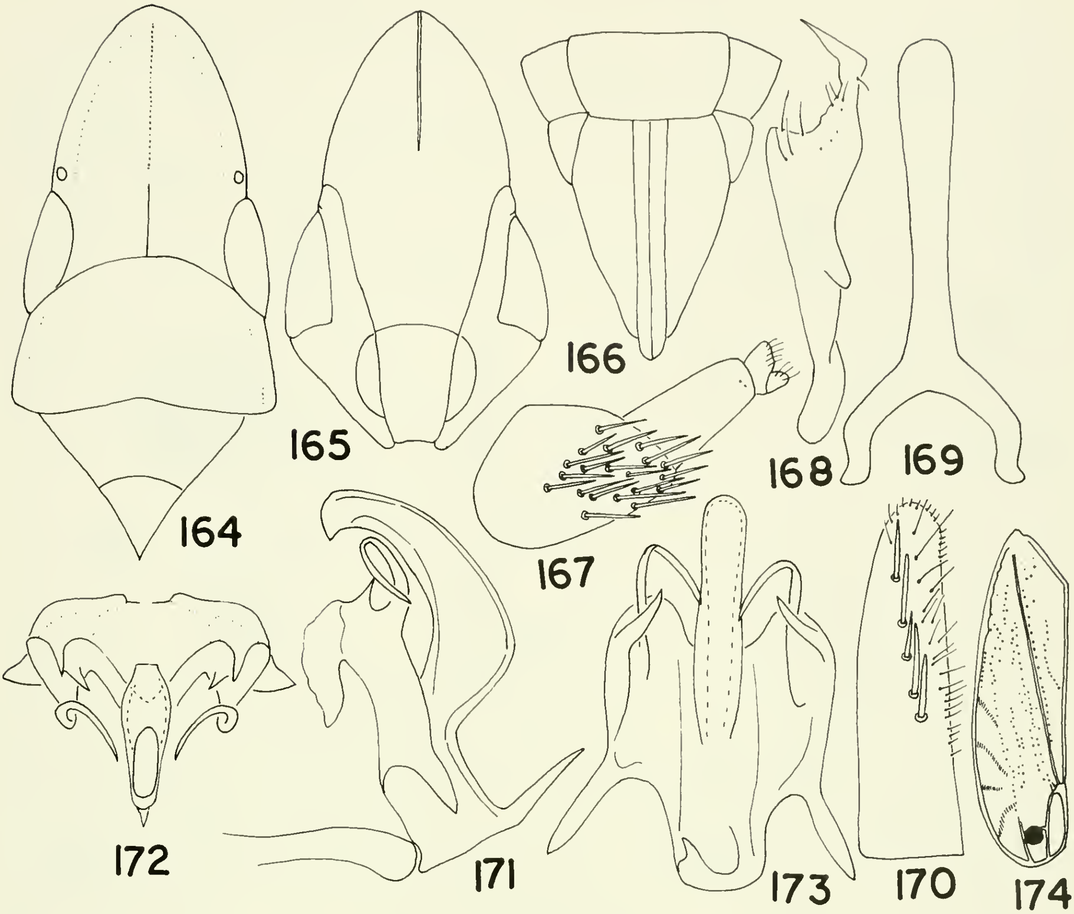
### *Sophonia complexa*, n. sp.

Figs. 175–185

Similar to *S. insignis* but more elongate. Vertex with median, crimson-colored line occupying about 0.66 area and apically bifid, short, slightly oblique, sublateral stripe on apical half of vertex orange. Forewing with fuscous spots (Fig. 178).

Apical 0.75 of vertex elongately rugulose, disc flat, margined by carina.

MALE GENITALIA.—Pygofer elongate, heavily setose, caudally rounded. Anal tube stout, long. Plate parallel-sided, about 3.5 times as long as wide, macrosetae restricted to apical 0.66. Apophysis of style short, apex avicephaliform. Connective with stem about three times as long as each arm. Aedeagus complex, each arm of dorsal apodeme with pair of ventrally directed processes, preatrium with caudally directed process, shaft tubular, slightly curved dorsally near apical 0.33, slightly flared.




Figs. 164–174. *Sophonia insignis* (Distant): 164, head and thorax; 165, face; 166, ovipositor; 167, male pygofer; 168, style; 169, connective; 170, male plate; 171–173, aedeagus, lateral, cephalic, and caudal views; 174, forewing.

FEMALE GENITALIA.—Hind margin of seventh sternum slightly concave.

MEASUREMENTS.—Male 5.32 (5.20–5.50) mm long, head 1.00 (0.97–1.02) mm wide, pronotum 1.06 (1.05–1.07) mm wide. Female 5.92 (5.80–6.00) mm long, head 1.10 (1.05–1.12) mm wide, pronotum 1.16 (1.15–1.17) mm wide.

SPECIMENS EXAMINED.—Holotype ♂, India: Meghalaya: Nongpoh, 762 m, 4.xi.1981, C. A. Viraktamath (UAS). Paratypes: 13 ♂, 4 ♀, data as in holotype but 7 ♂, 2 ♀ S. Viraktamath Coll. (1 ♂ and 1 ♀ in BMNH, IARI, USNM, and rest in UAS).

REMARKS.—This species is related to and resembles *S. insignis* as they share coloration and similar aedeagi. However, *S. complexa* differs from *S. insignis* in having the process of the dorsal apodeme bifid ventrally, a longer stem on the connective, and the crimson line of the vertex being forked apically.

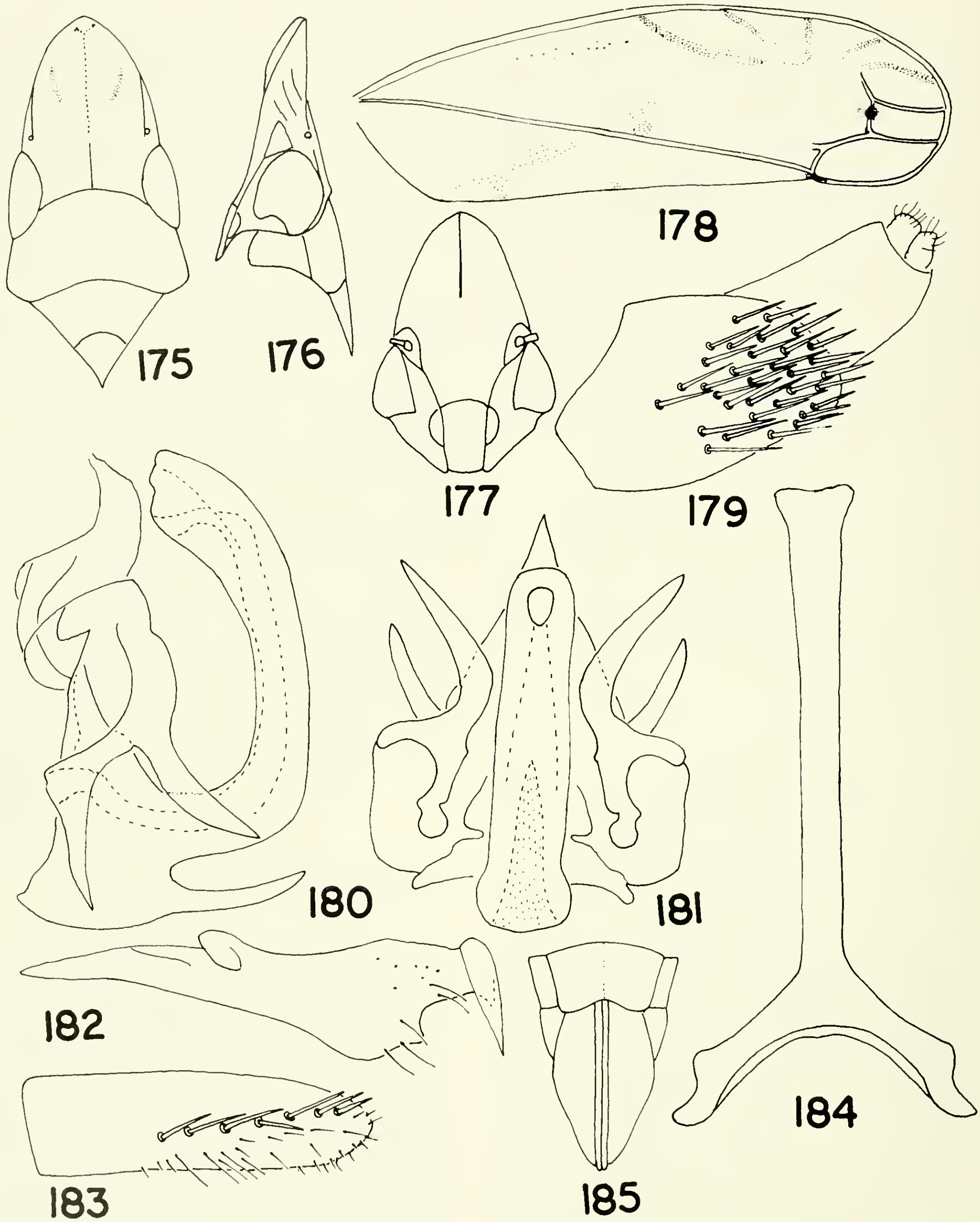
## *Sophonia modesta* (Distant), n. comb.

Figs. 186–197

*Kana modesta* Distant 1918b: 36. Lectotype ♂, India (BMNH, examined).

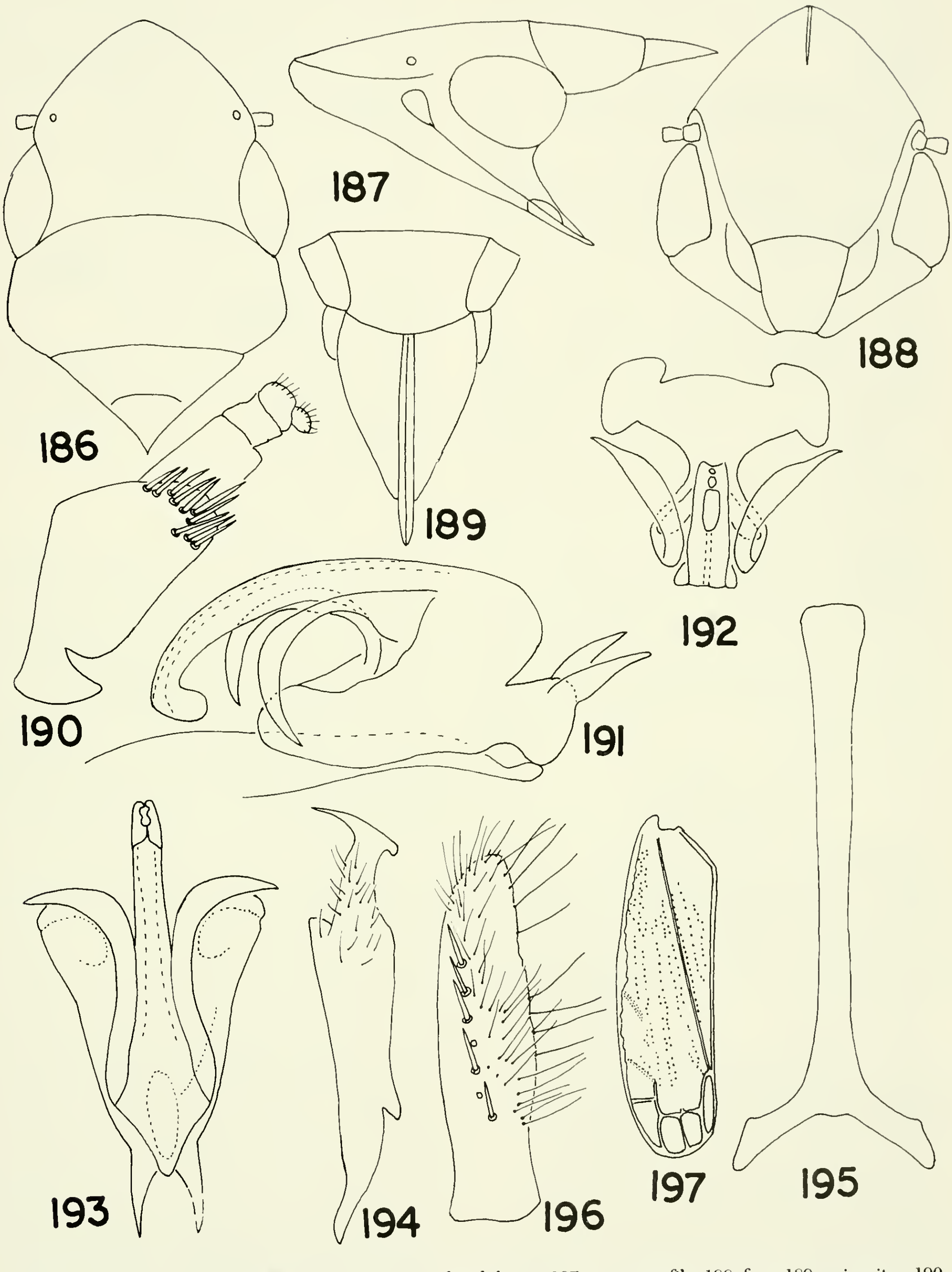
Pale yellow. Vertex of female creamy white, eyes lemon yellow. Forewing hyaline with brown stripe close to anal margin often reaching claval apex, apex of corium lemon yellow; costal margin with an anterior, long, oblique, median and a slightly oblique, posterior, transverse, brown fasciae; second apical cell with black spot, apical margin brownish.

Head slightly broader than pronotum. Vertex as long as wide between eyes, disc convex, apex subangular, granulose.




Figs. 175–185. *Sophonia complexa*, n. sp.: 175, head and thorax; 176, same, profile; 177, face; 178, forewing; 179, pygofer; 180, 181, aedeagus, lateral and caudal views; 182, style; 183, male plate; 184, connective; 185, ovipositor.

MALE GENITALIA.—Caudal lobe of pygofer rounded, without process. Anal collar well developed. Plate four times as long as wide. Preapical lobe of style small, rounded, apophysis setose on lateral margin, apical extension beaklike. Stem of connective four times as long as each arm. Aedeagus with preatrium short, pair of ventrocaudally directed processes, dorsal apodeme robust, each arm rounded; shaft tubular, slender, dorsally




Figs. 186–197. *Sophonia modesta* (Distant): 186, head and thorax; 187, same, profile; 188, face; 189, ovipositor; 190, pygofer; 191, aedeagus and part of connective, lateral view; 192, 193, aedeagus, dorsal and cephalic views; 194, style; 195, connective; 196, male plate; 197, forewing.

strongly curved anteriorly, apex ventrally directed with pair of elongate, basal processes that are directed dorsoanteriorly then laterally.

FEMALE GENITALIA.—Hind margin of seventh sternum slightly convex. Ovipositor fairly exceeding pygofer.

MEASUREMENTS.—Male 4.43 (4.40–4.50) mm long, head 1.08 (1.07–1.10) mm wide, pronotum 1.05 (1.03–1.08) mm wide. Female 5.20 (5.00–5.40) mm long, 1.24 (1.20–1.28) mm wide, pronotum 1.19 (1.15–1.25) mm wide.

SPECIMENS EXAMINED.—Lectotype ♂ labeled /South India, Madras, Coonoor, T. V. Campbell/ here designated (BMNH). India: Tamil Nadu: 3 ♂, 1 ♀, Kotagiri, 23.x.1975, C. A. Viraktamath; 1 ♀, Coonoor, 11.viii.1979, S. Viraktamath; 1 ♂, Wellington, 12.viii. 1979, S.V.; 5 ♀, Ootacamund, 2,350 m, 13. viii.1979, S.V. (UAS).

REMARKS.—*Sophonia modesta* externally resembles *S. bifida* in having a wider vertex, but they are only distantly related. It is related to *S. insignis* and *S. complexa* and differs from them in having paired preatrial processes and lacking processes on the dorsal apodeme. In these three species the stem of the connective is more than three times as long as each arm.

### *Sophonia bifida*, n. sp.
Figs. 198–207

Bright lemon yellow. Two spots on inner claval margin, one at midlength, another at apex, small costal patch about midlength, an outer, oblique and posterior, transverse fascia on costal area fuscous, large, round spot on second apical cell black. Hind tibial apical pecten black.

Head slightly narrower than pronotum. Disc of vertex about as long as wide between eyes, broadly rounded with apical area finely rugulose, posterior half polished. Frontoclypeus rather tumid. Second apical cell of forewing slightly narrowed caudally.

MALE GENITALIA.—Caudal margin of pygofer rounded with caudodorsal, short, stout, strongly hooked process and caudoventral, elongate, sharply pointed process; macrosetae forming single row. Anal tube large. Preapical lobe of style short, rounded, apophysis slender, rather hooked, apex beaklike. Arms of connective about as long as stem. Aedeagus with elongate preatrium; each arm of dorsal apodeme rounded; shaft tubular with basal pair of elongate processes extending to about 0.75 of length and with subapical pair of denticles on caudal margin.

MEASUREMENTS.—Male 4.50 mm long, head 1.07 mm wide, pronotum 1.10 mm wide. Female 5.30 mm long, head 1.25 mm wide, pronotum 1.25 mm wide.

SPECIMENS EXAMINED.—Holotype ♂, India: West Bengal: Darjeeling, 2,176 m, 11.xi.1981, C. S. Wesley (UAS). Paratype ♀, India: West Bengal: Kalimpong, 1,370 m, 29.x.1981, S. Viraktamath (UAS).

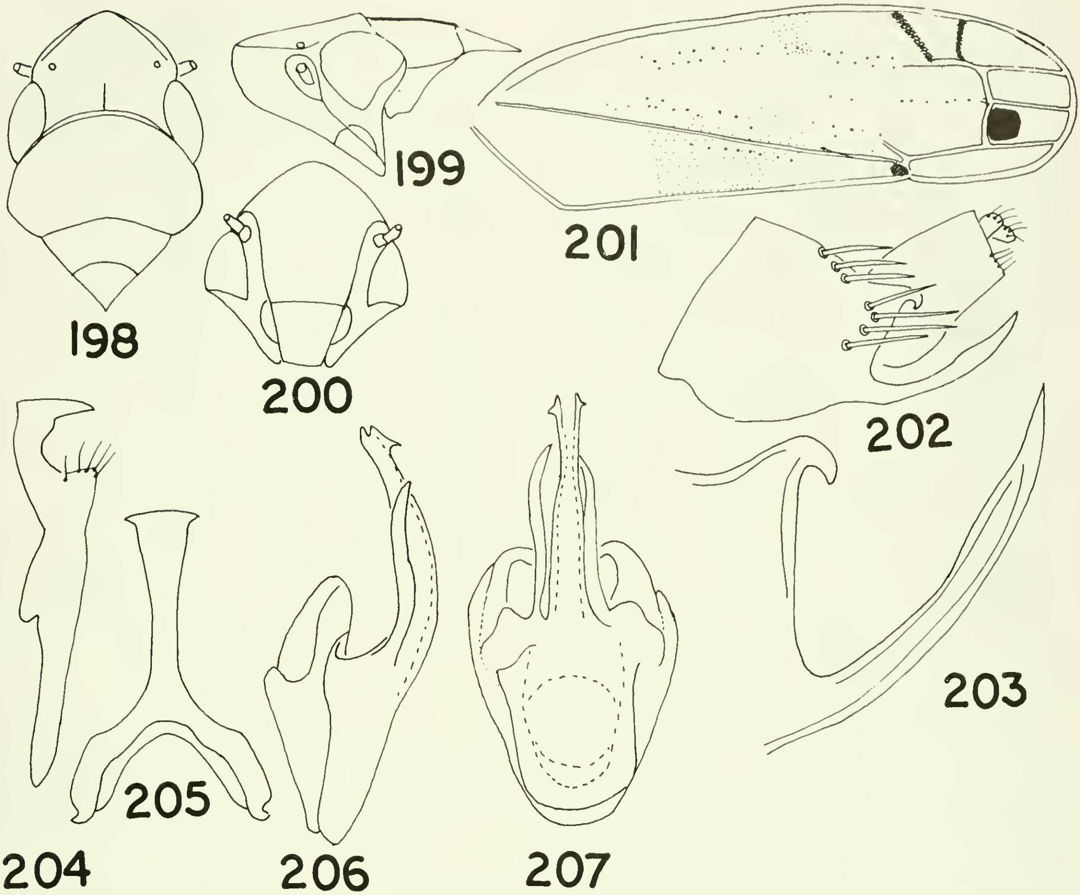
REMARKS.—Although the shape of the head is similar to that in *S. modesta*, *S. bifida* occupies an isolated place in *Sophonia*. The peculiar pygofer process and aedeagus differentiate it from all other species.

### *Sophonia complicata*, n. sp.
Figs. 208–220

Whitish yellow. Area surrounding ocelli, lateral-most area of pronotum lemon yellow. Second apical cell with round, black spot. Costa with outer, oblique fascia, posterior, transverse fascia near apex, and apical margin of forewing fuscous. In a few specimens, median area of clavus pale fuscous, which meets fuscous stripe on claval suture and continues angularly across wing where it is joined by an oblique, fuscous fascia from costa. Hind tibial pecten fuscous.

Vertex more conically produced, disc convex with median carina in apical half and apical area rugulose, rugae crisscrossing. Vertex of female distinctly longer than male. Head wider than pronotum.

MALE GENITALIA.—Pygofer with caudodorsal angle roundly produced, with excavation below which long, slender process arises, directed caudally, upcurved at right angles at midlength, apex slightly hooked, bearing spinelike branch at base. Anal tube robust, slightly exceeding pygofer lobe, but not pygofer process. Plate 3.75 times as long as wide. Style with elongate, slender, preapical lobe, apophysis slender avicephaliform. Stem of connective more than twice as long as each arm. Aedeagus complex, two arms of dorsal apodemes well separated, winglike, completely covering entire length of shaft laterally, each arm with dorsomedian, caudal, and caudoventral, long processes; dorsomedian




Figs. 198–207. *Sophonia bifida*, n. sp.: 198, head and thorax; 199, same, profile; 200, face; 201, forewing; 202, male pygofer; 203, pygofer process; 204, style; 205, connective; 206, 207, aedeagus, lateral and caudal views.

process curves caudally, caudal process directed anteriorly and in contact with dorsomedian process, caudoventral process crosses over caudad of shaft, thus enclosing it; shaft depressed, strongly curved anteriorly, expanded, and hoodlike.

MEASUREMENTS.—Male 4.40 (4.30–4.50) mm long, head 0.92 (0.90–0.95) mm wide, pronotum 0.94 (0.90–0.95) mm wide. Female 4.88 (4.60–5.10) mm long, head 1.01 (0.97–1.05) mm wide, pronotum 1.02 (1.00–1.05) mm wide.

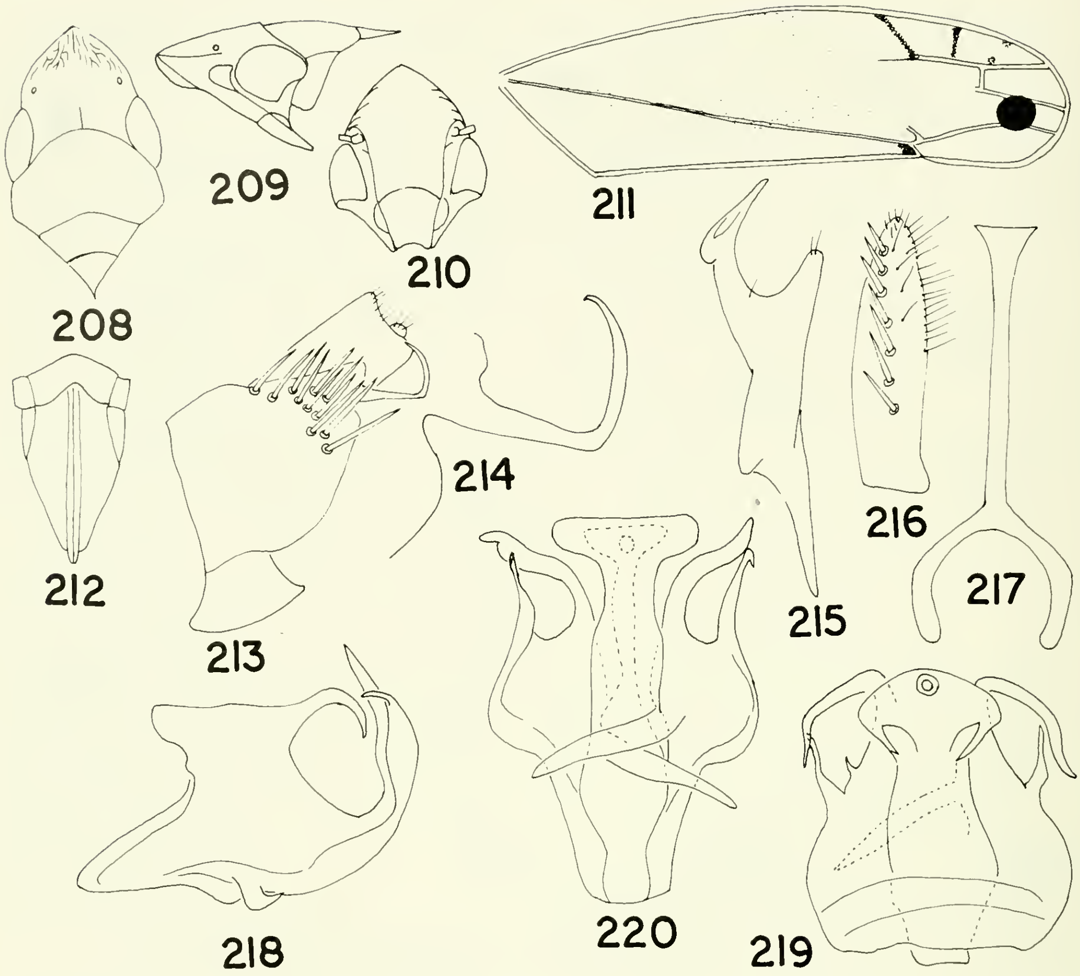
SPECIMENS EXAMINED.—Holotype ♂, India: Mizoram: Lungleh, 23.xi.1981, C. S. Wesley (UAS). Paratypes: 15 ♂, 16 ♀, India: Mizoram: Aizawl, 18.xi.1981, C. S. Wesley; 3 ♂, 1 ♀, Lungleh, 22–24.xi.1981, C. S. Wesley; Meghalaya: 2 ♀, Cherrapunji, 1,299 m, 3.xi.1981, C. A. Viraktamath; 1 ♀, Shillong, 1,961 m, 3.xi.1981, S. Viraktamath (1 ♂ and 1 ♀ paratypes in BMNH, IARI, USNM, ZSI, and rest in UAS).

REMARKS.—The complex nature of the aedeagus and the slender, long pygofer process distinguish this species from other species of *Sophonia*.

## Genus *Nirvana* Kirkaldy

*Nirvana* Kirkaldy 1900d: 293. Type species: *Nirvana pseudommatos* Kirkaldy, by original designation and monotypy.

Vertex longer than width between eyes, disc depressed apically, with median ridge. Ocelli situated laterally mesad of submarginal carina. Face slightly depressed basally, frontoclypeus with short, apical, median ridge and lateral, oblique rugae weakly developed. Second apical cell of forewing narrowed apically. Hindwing with three apical, closed cells.




Figs. 208–220. *Sophonia complicata*, n. sp.: 208, head and thorax; 209, same, profile; 210, face; 211, forewing; 212, ovipositor; 213, male pygofer; 214, pygofer process; 215, style; 216, male plate; 217, connective; 218–220, aedeagus, lateral, caudal, and dorsal views.

Hind tibial spinulation $R_1$ 20 ± 2, $R_2$ 12 ± 1, $R_3$ 12 ± 2.

MALE GENITALIA.—Pygofer lobe caudally, bluntly conical or rounded, with ventral, short or long process, caudal area with numerous macrosetae. Plate parallel-sided, elongate, more than five times as long as wide near middle, with oblique row of macrosetae in apical 0.66 and hairlike setae. Style with well-developed preapical lobe; apophysis short, apical extension more than twice length, beaklike. Aedeagal shaft tubular, with or without processes, dorsal apodeme slender in cephalic view, U-shaped; gonopore apical.

REMARKS.—*Nirvana* and *Sophonia* are closely related and are difficult to separate by external characters. *Nirvana* has a simple dorsal apodeme, usually without processes, whereas in *Sophonia* it is complex with more elaborate processes; the male plate in *Nirvana* is narrow and elongate compared to *Sophonia*. Specimens of *N. pseudommatos* were not available for the study, and hence the genus is only tentatively defined here.

Key to Species of *Nirvana*

1. Vertex with median, white stripe and lateral, orange or lemon yellow, submarginal stripe; aedeagal shaft with two slender, lateral, long, ventral processes directed ventrally (Figs. 225, 226) . . . . . . . . . . . . . . . . . . . . . . . . *pallida* Melichar

— Vertex with black line or lines or with orange, submarginal stripes traversing on pronotum and

scutellum and forewing; aedeagus without processes (male of *pseudommatos* is not known) . . . 2

2(1). Vertex, pronotum, scutellum traversed by pair of orange stripes (Fig. 256); male pygofer caudally produced into an acute, dorsally curved process (Fig. 261); anal tube with two stout spines (Fig. 262) .......... *peculiaris*, n. sp.

— Vertex, pronotum, and scutellum traversed by black lines or stripes; male pygofer and anal tube unarmed (not known in *pseudommatos*) ....... 3

3(2). Vertex, pronotum, scutellum, and anal margin of forewing traversed by broad, black stripe .... 4

— Vertex of head and pronotum traversed by three black stripes; scutellum by a median, black line; apex of vertex with blackish brown spot connected by the stripes .... *pseudommatos* Kirkaldy

4(3). Median stripe with irregular margins (Figs. 233, 234); spot on second apical cell of forewing small (Fig. 243); dorsal apodeme of aedeagus simple (Fig. 240) .................. *suturalis* Melichar

— Median stripe with an even margin (Fig. 244); spot on second apical cell of forewing large (Fig. 248) extending to first apical cell; dorsal apodeme of aedeagus with a basal, short process (Fig. 254) ...................... *striata*, n. sp.

### *Nirvana pallida* Melichar
Figs. 221–232

*Nirvana pallida* Melichar 1903b: 166. Syntype ♂, ♀, Sri Lanka (not examined).

*Quercinirvana bengalensis* Ahmed & Mahmood 1970: 263. Holotype ♂, Bangladesh (University of Karachi, not examined). *New synonymy*.

Coloration as described by Melichar (1903b). The median, white stripe of vertex may be obscured in some specimens.

Head as wide as or slightly narrower than pronotum. Vertex 1.5 to 2.0 times as long as width between eyes, disc slightly depressed. Clypellus convex.

MALE GENITALIA.—Pygofer lobe caudally rounded with marginal macrosetae, ventral process long, dorsally directed with rounded apex. Plate narrowed caudally with bluntly conical apex. Preapical lobe of style rounded, stout. Stem of connective longer than arms. Aedeagus with dorsal apodeme well developed, consisting of two arms and forming a U, shaft tubular, curved slightly with short, spinelike, laterally directed, terminal processes and long, unpaired, ventrally directed, subapical process.

FEMALE GENITALIA.—Hind margin of seventh sternum rather straight. Ovipositor slightly exceeding pygofer.

MEASUREMENTS.—Male 4.80 (4.60–5.00) mm long, head 0.94 (0.90–0.98) mm wide, pronotum 1.02 (0.95–1.08) mm wide. Female 5.65 (5.5–5.80) mm long, head 1.06 (1.05–1.07) mm wide, pronotum 0.93 (0.88–0.98) mm wide.

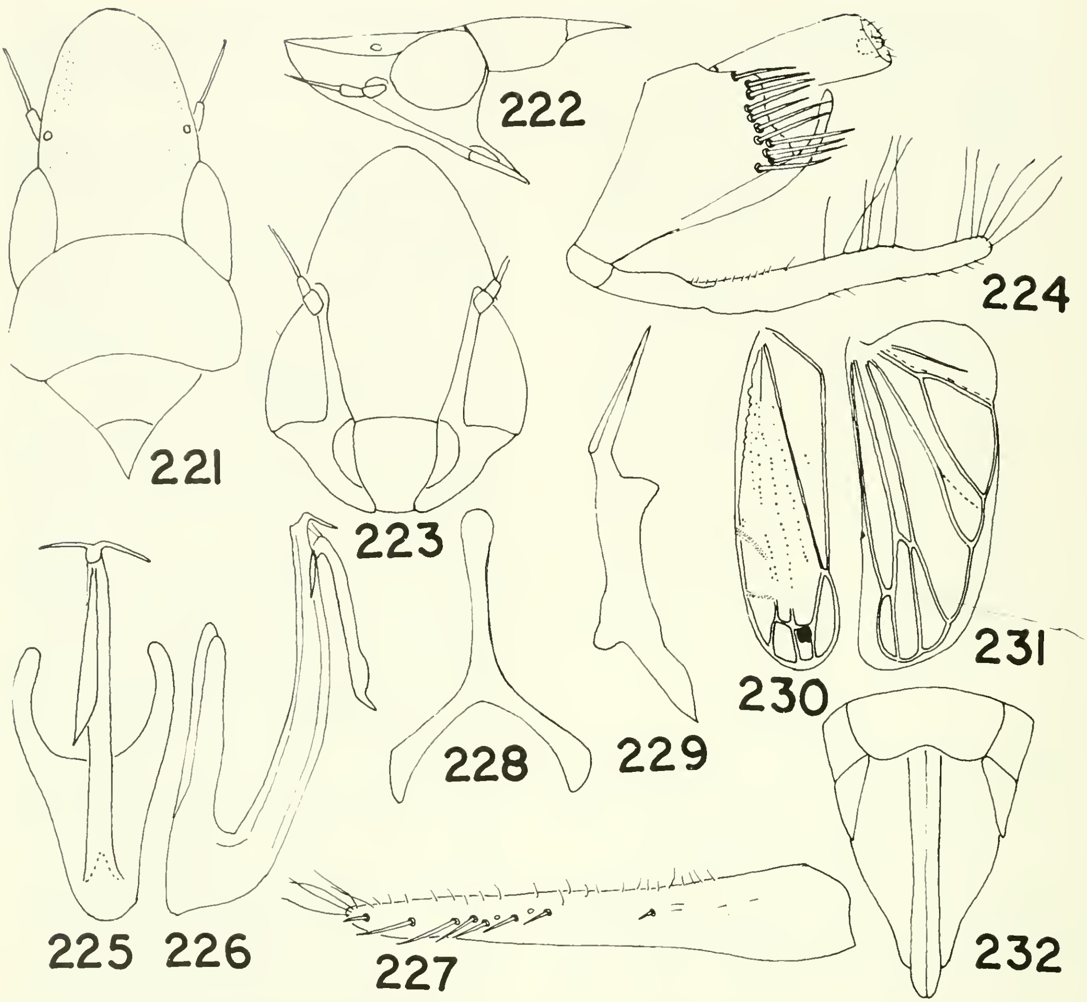
SPECIMENS EXAMINED.—India: 203 ♂, 274 ♀, collected from the states of Andhra Pradesh, Haryana, Karnataka, Kerala, Maharashtra, Meghalaya, Mizoram, Sikkim, Tamil Nadu, and West Bengal from January to December, from sea level (Cochin in Kerala) to 2,250 m (Kodaikanal in Tamil Nadu) above sea level. Nepal: 1 ♀, Sarankot, 17.xi.1979, I. Dworakowska. Sri Lanka: 1 ♀, Peradeniya, 23.viii.1979, I. Dworakowska (UAS).

REMARKS.—This species is the most common and most frequently encountered Nirvaninae on the Indian subcontinent. It breeds on newly emerged leaves of *Tecoma stans*, *Duranta* sp., *Vitis vinifera*, beans, pigeon pea, etc. The species is identified based on the description and illustrations provided by Melichar (1903b). No other species of Nirvaninae has the color and elongate male plate with two short, lateral, and caudal processes on the aedeagal shaft. The synonymy of *Q. bengalensis* is based on the illustrations of male genitalia of the species provided by Ahmed and Mahmood (1970) and on the specimens collected from northeastern India. None of the specimens collected, however, has "a pair of median stripes blackish pale to pale brown, running from anterior tip of crown to posterior margin of pronotum." Based on the illustrations, *Pseudonirvana rubrolimbata* Kuoh & Kuoh may also prove to be a synonym of this species.

### *Nirvana suturalis* Melichar
Figs. 233–243

*Nirvana suturalis* Melichar 1903b: 166. Holotype ♀, Sri Lanka (ZMHU, examined).

Yellow. Median, longitudinal, black stripe traversing vertex, pronotum, scutellum and continued along inner margin of clavus of forewing, with uneven, lateral margins and extending angularly on corium beyond clavus (stripe constricted a short distance from apex of vertex in Indian specimens but not in holotype female) (Figs. 233, 234). First, second, and outer margin of fourth apical cells of forewing dark brown, costal margin with piceous, oblique fascia about 0.25 distance from apex; second apical cell with black spot. Ventral surface of body creamy white.




Figs. 221–232. *Nirvana pallida* Melichar: 221, head and thorax; 222, same, profile; 223, face; 224, male pygofer; 225, 226, aedeagus, caudal and lateral views; 227, male plate; 228, connective; 229, style; 230, forewing; 231, hindwing; 232, ovipositor.

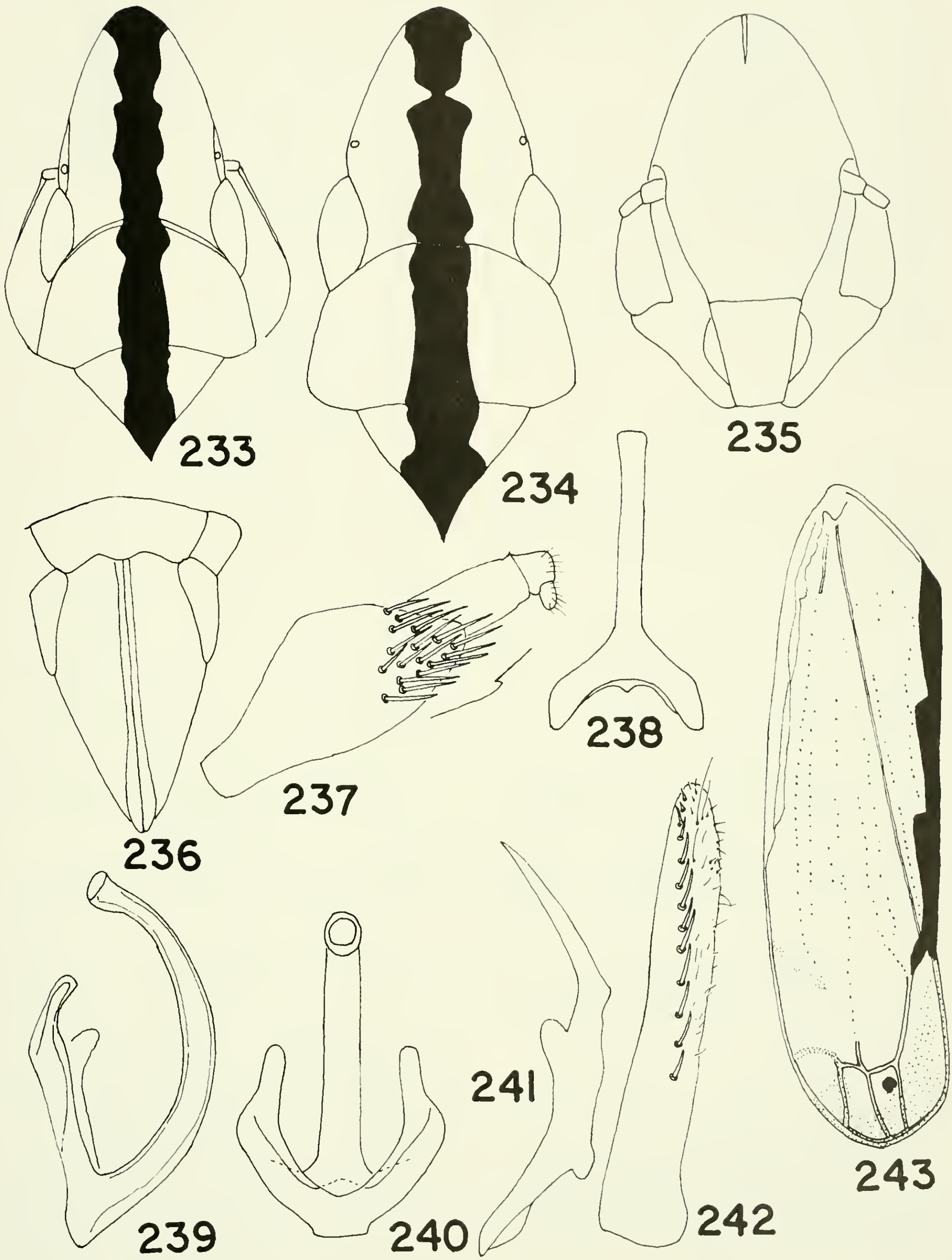
Head narrower than pronotum. Vertex about 1.5 times as long as width between eyes, with median, longitudinal groove not reaching apex, rugulose in anterior half, posterior half polished.

MALE GENITALIA.—Pygofer bluntly conical caudally, with ventral, short notch, macrosetae confined to apical 0.33 area. Plate more than six times as long as wide. Preapical lobe of style rounded, relatively slender. Stem of connective twice as long as length of each arm. Aedeagus with short preatrium, shaft tubular, slightly curved, each arm of dorsal apodeme wider in middle.

FEMALE GENITALIA.—Hind margin of seventh sternum concave with median, short protuberance. Ovipositor exceeding pygofer.

MEASUREMENTS.—Male 4.20 (4.00–4.30) mm long, head 0.85 (0.83–0.88) mm wide, pronotum 0.88 (0.85–0.90) mm wide. Female 4.74 (4.40–5.00) mm long, head 0.90 (0.80–0.95) mm wide, pronotum 0.93 (0.88–0.98) mm wide.

SPECIMENS EXAMINED.—Holotype ♀ labeled /Type/ /7042/ /Ceylon, Nietr./ /*suturalis*, det. Melichar/ /*Nirvana suturalis* Melichar/ (ZMHU). India: 48 ♂, 66 ♀, collected from the states of Karnataka, Kerala,




Figs. 233–243. *Nirvana suturalis* Melichar: 233, head and thorax of holotype female; 234, female from India; 235, face; 236, ovipositor; 237, male pygofer; 238, connective; 239, 240, aedeagus, lateral and cephalic views; 241, style; 242, male plate; 243, forewing.

and Tamil Nadu from January to December, at an altitudinal range of 534 m (Jog Falls in Karnataka) to 2,350 m (Ootacamund in Tamil Nadu) above mean sea level.

REMARKS.—This is the second most commonly collected Nirvaninae in southern India. *Nirvana suturalis* and *N. striata* are very closely related. Both differ from other species of *Nirvana* and *Sophonia* in having a broad, black, median stripe running from the apex of the vertex to the corium, but the stripe is not as broad as in species of *Chudania*. *Nirvana suturalis* has a serrated lateral margin to the median stripe compared to the smoother lateral margin in *N. striata*.

### *Nirvana striata*, n. sp.
Figs. 244–255

Coloration as in *N. suturalis*, median stripe more or less of uniform width and even margined, black spot on second apical cell of forewing, larger than in *N. suturalis*, extending to first apical cell.

Head narrower than pronotum. Vertex slightly longer than width between eyes, anterior half sparsely rugulose. Pronotum slightly more than 1.5 times as wide as long, longer than scutellum.

MALE GENITALIA.—Pygofer bluntly conical with macrosetae confined to caudal 0.33 area, ventral margin with short, spinelike process. Plate caudally rounded, about seven times as long as wide. Style with rounded preapical lobe, apical extension of apophysis beaklike and long. Stem of connective twice as long as each arm. Aedeagus with shaft strongly curved (more than in *N. suturalis*), apex abruptly directed cephalad and with membranous area; each arm of dorsal apodeme with basal, short process.

FEMALE GENITALIA.—Hind margin of seventh sternum straight. Ovipositor exceeding pygofer.

MEASUREMENTS.—Male 4.90 (4.80–5.00) mm long, head 0.98 (0.95–1.00) mm wide, pronotum 1.06 (1.05–1.08) mm wide. Female 5.46 (5.30–5.60) mm long, head 1.08 (1.05–1.10) mm wide, pronotum 1.12 (1.08–1.13) mm wide.

SPECIMENS EXAMINED.—Holotype ♀, India: West Bengal: Kurseong, 1,483 m, 22.x.1981, S. Viraktamath (UAS). Paratypes: India: Uttar Pradesh: 1 ♀, Mussoorie, 2,005 m, 27.iv.1975, C. A. Viraktamath; Himachal Pradesh: 3 ♀, Simla, 2,133 m, 14.x.1979, C. A. Viraktamath; West Bengal: 3 ♂, 3 ♀, Kurseong, 1,483 m, 22.x.1981, S. Viraktamath (1 ♂, 1 ♀) and C. A. Viraktamath (2 ♂, 2 ♀); 1 ♀, 15 km E of Kalimpong, 1,780 m, 27.x.1981, S. Viraktamath; 1 ♂, 2 ♀, 8 km E of Kalimpong, 1,768 m, 29.x.1981, C. A. Viraktamath (1 ♂ and 1 ♀ paratypes in BMNH, USNM, and rest in UAS).

REMARKS.—See *N. suturalis*.

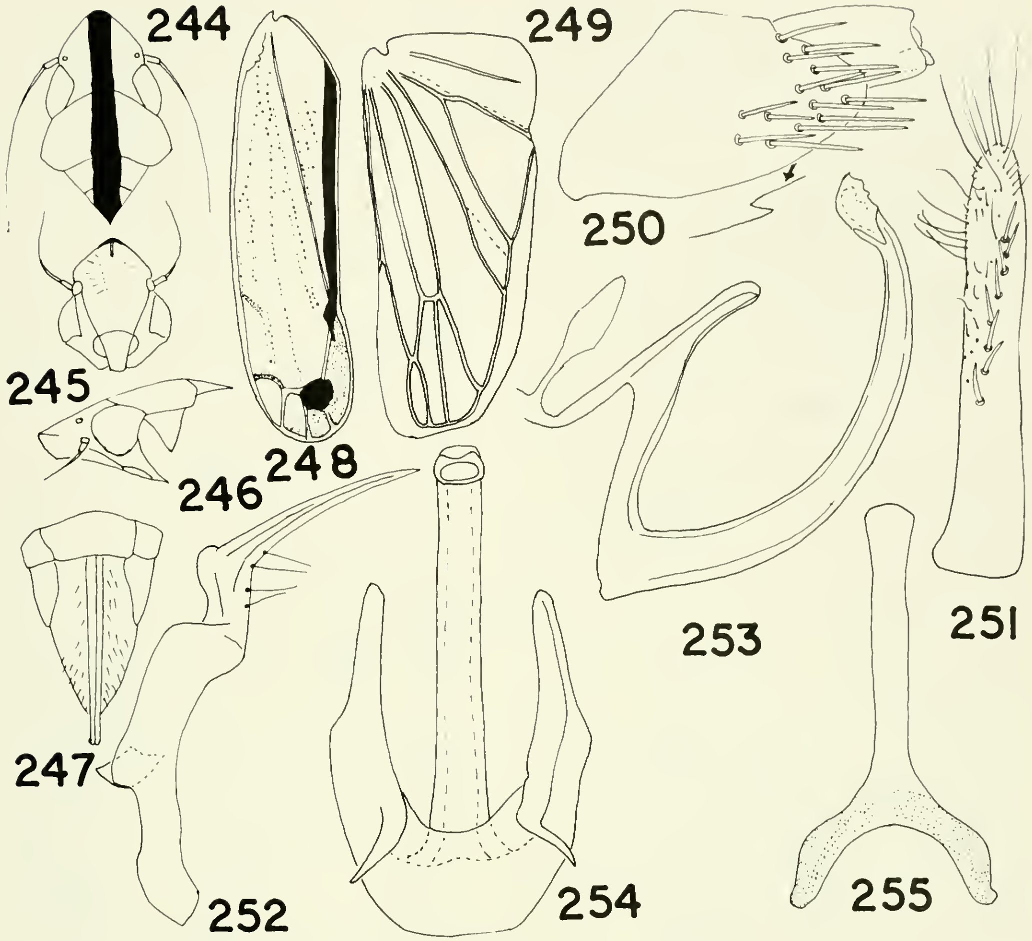
### *Nirvana peculiaris*, n. sp.
Figs. 256–267

Yellow. Small, black spot at apex of vertex visible both dorsally and ventrally (absent in female from Shillong). Fuscous, median stripe extending posteriorly to 0.25 length (absent in some females). Lateral, orange stripe on vertex mesad of ocelli, continued on pronotum, scutellum and then on to inner claval margin where they converge and continue to apex of clavus; outer margin of stripe on clavus often fuscous. Transverse spot at apex of clavus, small spot at apex of inner, anteapical cell, and anterior, oblique fascia from costa fuscous. Black spot on each caudodorsal angle of male pygofer.

Head as wide as pronotum or slightly narrower. Disc of vertex depressed with rolled-up, sharp margin, basal half with median sulcus, apical half with a carina, apical half of disc very finely pitted, posterior half with minute rugulae on polished surface.

MALE GENITALIA.—Pygofer elongate, narrowed caudally to acute, dorsally curved process. Anal collar elongate, anterior margin armed with two pronglike processes on each side. Setae on pygofer confined to caudodorsal area where it articulates with anal tube. Male plate elongate, 5.4 times as long as median width, macrosetae and hairlike setae confined to apical half. Connective robust, stem broad, and arms as long as stem. Apophysis of style fairly long. Aedeagus with dorsal apodeme poorly developed, shaft tubular, narrowed caudally, strongly curved dorsally near apex and with elongate, caudoventrally directed process and two lateral, anteriorly directed processes surrounding small gonopore.

MEASUREMENTS.—Male 5.80 (5.70–5.90) mm long, head 1.23 (1.22–1.25) mm wide, pronotum 1.24 (1.22–1.25) mm wide. Female 7.40 (7.00–7.80) mm long, head 1.50 (1.45–




Figs. 244–255. *Nirvana striata*, n. sp.: 244, head and thorax; 245, face; 246, profile; 247, ovipositor; 248, forewing; 249, hindwing; 250, male pygofer; 251, male plate; 252, style; 253, 254, aedeagus, lateral and cephalic views; 255, connective.

1.55) mm wide, pronotum 1.54 (1.50–1.60) mm wide.

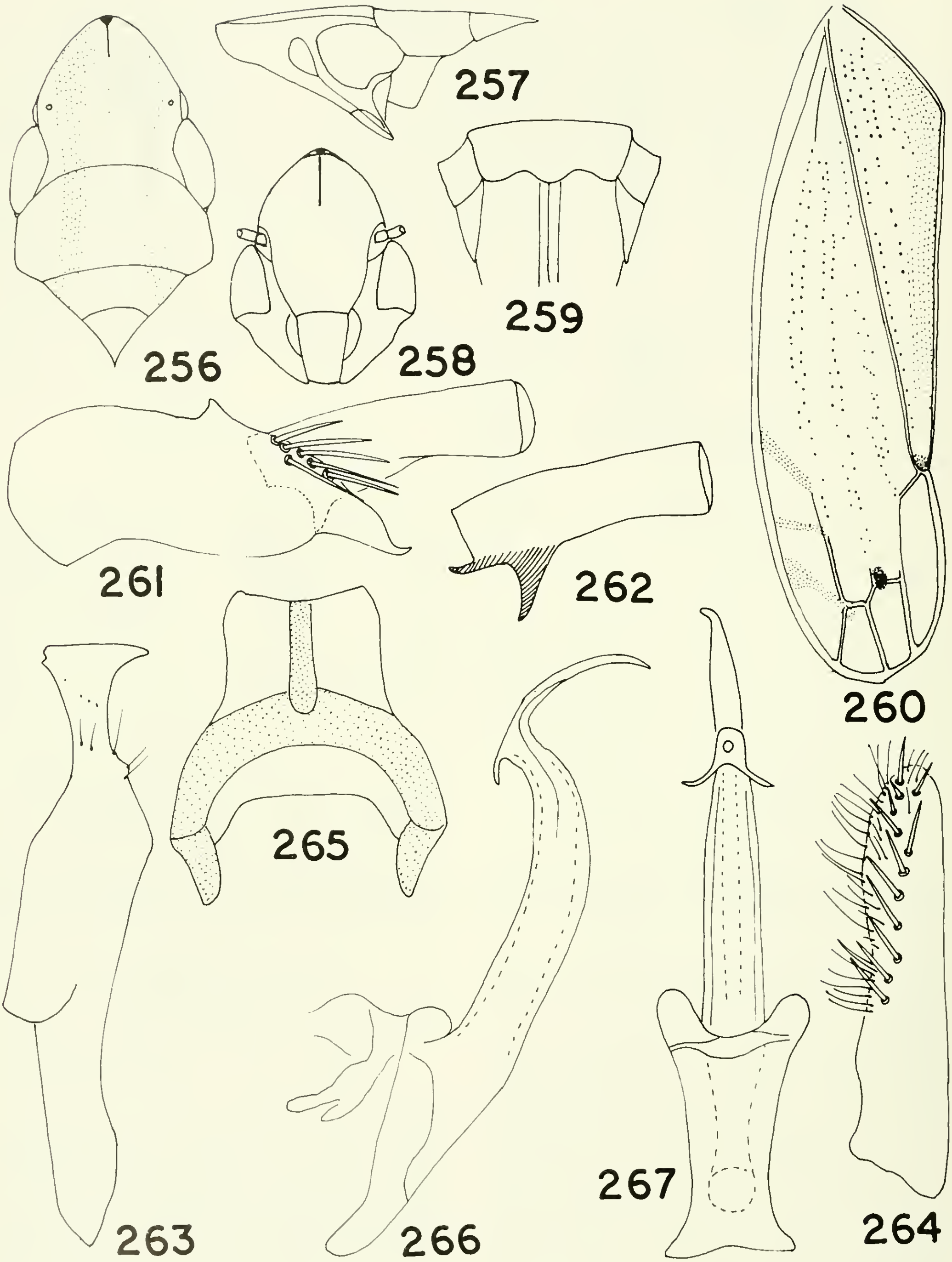
SPECIMENS EXAMINED.—Holotype ♂, India: Mizoram: Aizawl, 18.xi.1981, C. S. Wesley (UAS). Paratypes: India: Mizoram: 2 ♂, 4 ♀, Aizawl, 18.xi.1981, C. S. Wesley; 1 ♂, 2 ♀, Lungleh, 23.xi.1981, C. S. Wesley; Meghalaya: 1 ♀, Shillong, 1,961 m, 3.xi.1981, S. Viraktamath (1 ♀ and 1 ♀ paratypes in BMNH; 1 ♀ paratype in IARI, USNM, ZSI, and rest in UAS).

REMARKS.—This species is unique among Nirvanini in having an armed tenth segment. In coloration it resembles species of *Kana*, especially *K. fasciata*, but it differs from those species in having three apical cells in the hindwing and unique male genitalia.

## *Ophiuchus* Distant

*Ophiuchus* Distant 1918b: 33. Type species: *Ophiuchus princeps* Distant, by original designation and monotypy.

Pale yellow with bright, contrasting coloration of black and red or pink. Head about as wide as pronotum, spatulate, disc of vertex depressed in middle, margined by carina, lateral margin of vertex straight in front of eyes to ocelli where it is widened and then slightly narrowed to apex. Face with five lateral ridges, concave medially, with short, median carina near apex. Pronotum twice as wide as median length, disc minutely, transversely rugose. Hindwing with three closed apical cells. $R_2$ of hind tibia with 12 spines.




Figs. 256–267. *Nirvana peculiaris*, n. sp.: 256, head and thorax; 257, same, profile; 258, face; 259, female seventh sternum; 260, forewing; 261, male pygofer; 262, male tenth segment; 263, style; 264, male plate; 265, connective; 266, 267, aedeagus, lateral and cephalic views.

Male pygofer elongate, heavily macrosetose and with caudal, hooklike process. Valve semicircular. Plate rounded apically, macrosetae scattered and confined to caudal 0.40. Style appearing like partially closed fist. Aedeagus large, poorly sclerotized, with ventral, platelike process, shaft short, cylindrical with large gonopore.

REMARKS.—This genus appears related to *Sophonia* and *Nirvana* with which it shares general facies of the head. The peculiarly shaped style and scattered macosetae on the male plate distinguish this genus.

### *Ophiuchus princeps* Distant
Figs. 268–276

*Ophiuchus princeps* Distant 1918b: 34. Lectotype ♂, India (BMNH, examined).

Pale yellow. Vertex laterally margined by black line that does not reach apex, black, median, longitudinal line does not reach apex. Eyes centrally fuscous surrounded by red. Ocelli red. Face ochraceous with lateral infoldings black. Pronotum sanguineous with submarginal, anterior, transverse, whitish spot. Scutellum anteriorly marked with fuscous band with backward, lateral projections. Base of forewing fuscous, apical 0.33 with an irregular, pink spot margined by fuscous, rest yellowish.

Head shorter than combined length of pronotum and scutellum (36:44). Pronotum shorter than scutellum (21:23). Face longer than wide.

MALE GENITALIA.—Pygofer elongate, lobe covered with numerous stout setae and terminated by curved, hooklike process. Valve semicircular. Plate elongate, with angulate projection on lateral margin near apex. Style flat, preapical lobe with few setae, apophysis with two angular projections and apically pointed. Aedeagus with very short, dorsal apodeme, elongate, platelike, ventral process, armed with median ridge and two caudal, spinelike processes on its laterocaudal angles, shaft short, cylindrical, with large, round gonopore and with pair of lateral processes about its midlength.

MEASUREMENTS.—Male 4.60 mm long, head 1.07 mm wide, pronotum 1.05 mm wide.

SPECIMEN EXAMINED.—Lectotype ♂ labeled /Travancore/ /Distant Coll. 1911–383/ /*Ophiuchus princeps* Dist., type/ here designated (BMNH).

REMARKS.—This species has a very distinctive coloration not possessed by any other species of Nirvaninae known from the Indian subcontinent nor by any other species of *Ophiuchus* known from the Oriental region and Australia. The male genitalia of *Ophiuchus* species except *O. distanti* Evans (1973: Fig. 5B) are not sufficiently known to suggest any relationships among them. Judging from the illustrations of *O. distanti*, it does not appear to be related to *O. princeps*.

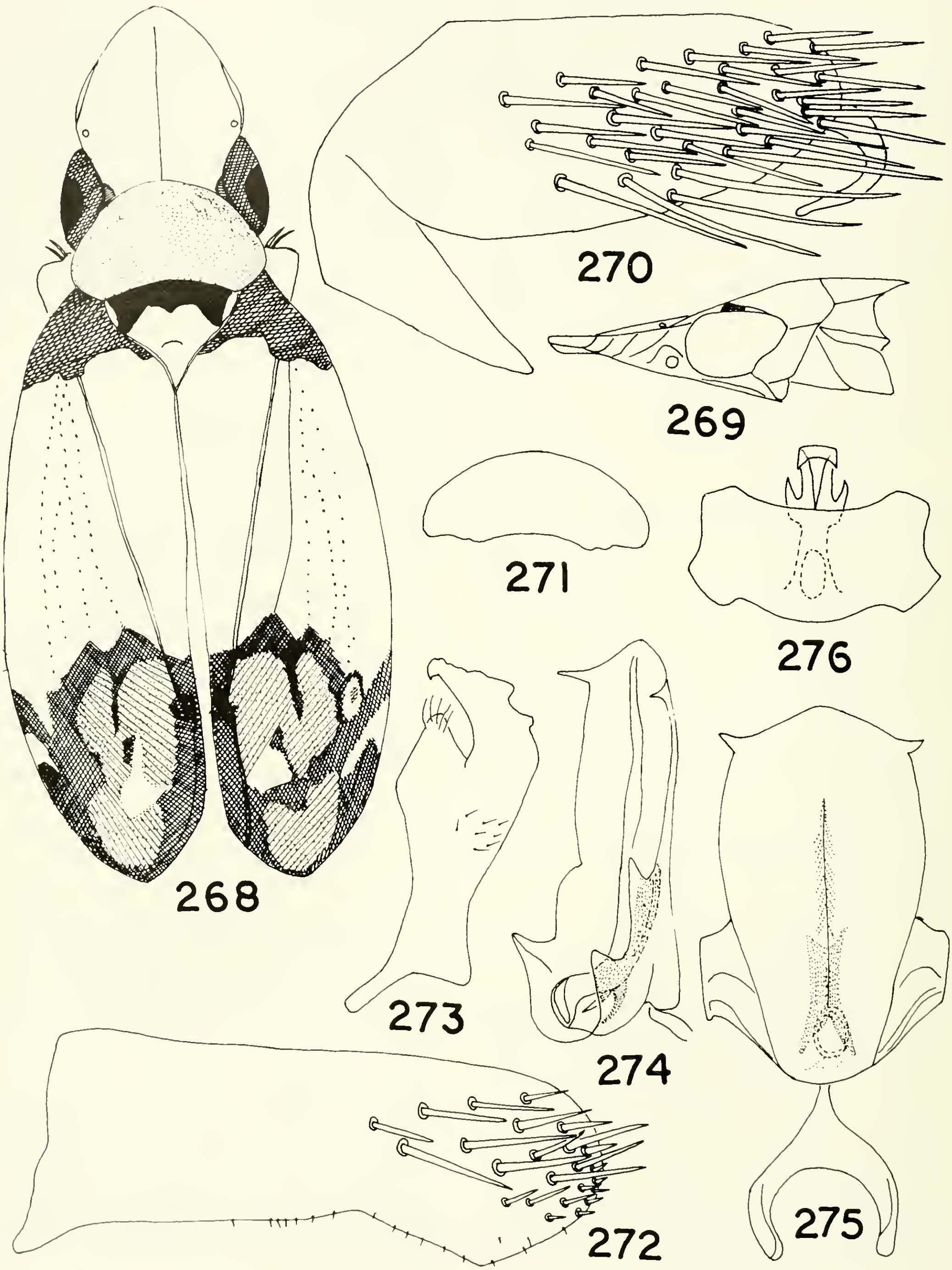
## Tribe Occinirvanini

Body elongate, slightly depressed. Head produced anteriorly, spatulate. Face horizontal, frontoclypeus and clypellus either flat (*Occinirvana* Evans) or convex; facial sulci deep, prominent; face longer than wide, genae laterally emarginate below eyes, lora fairly prominent.

Antennae arising close to anterior margin of head. Vertex elongate, with median sulcus and transverse ridge or carina across ocelli, which are situated on disc of vertex closer to anterior than to posterior margin. Lateral margin of pronotum rounded, without carina, rather parallel-sided. Forewing with complete and prominent venation; at least three cross-veins reaching vein R from costal margin; anteapical cells three, outer anteapical cell half as long as median, inner anteapical cell open basally; apical cells four; appendix distinct, often extending around apical margin as in *Omaranus* Distant. Hindwing with three apical cells. Hind femoral spinulation 2+1+0. Hind basitarsus with six platellae (in *Omaranus*).

Male genitalia is of deltocephaline type. Pygofer laterally not fused with valve, lobe covered by stout setae. Valve triangular. Plates triangular with stout macrosetae. Style deltocephaline type with well-developed, preapical lobe and fingerlike apophysis. Connective Y-shaped with diverging arms. Aedeagus simple, with large gonopore, articulated with connective.

REMARKS.—The tribe, judged from the structural features, is not closely related to either Nirvanini or Balbillini. It has several deltocephaline features, especially the male genitalia.




Figs. 268–276. *Ophiuchus princeps* Distant: 268, habitus; 269, profile; 270, male pygofer; 271, male valve; 272, male plate; 273, style; 274, aedeagus, lateral view; 275, aedeagus and connective, ventral view; 276, aedeagus, cephalic view.

### Genus *Omaranus* Distant

*Omaranus* Distant 1918b: 5. Type species: *Omaranus typicus* Distant, by original designation and monotypy.
*Didius* Distant 1918b: 36. Type species: *Didius sexualis* Distant, by original designation and monotypy.

Sexually dimorphic. Head narrower than pronotum in male, wider than pronotum in female. Vertex with median carina in apical half, sulcus in basal half. Face longer than broad, frontoclypeus tumid. Clypellus longer than broad; frontoclypeus, lora, genae, and clypellus with scattered, short setae. Pronotum gradually widened posteriorly in male, parallel-sided and with faint, median ridge near posterior half in female; posterior margin strongly inwardly concave; disc flattish in female, slightly raised posteromedially in male, lateral margins not carinate. Male forewing exceeds abdomen, appendix runs around apical margin, with four apical and three anteapical cells; hindwing well developed with three apical cells. Female forewings cover only three basal, visible, abdominal terga, while hindwings cover two basal, visible terga; appendix wanting. Hind tibial spinulation $R_1$ $16 \pm 2$, $R_2$ $10 \pm 1$, $R_3$ 3. Hind basitarsus shorter than combined length of second and third tarsi and terminated by six platellae.

Male pygofer without processes. Tenth segment stout, rather short. Ovipositor not exceeding pygofer.

REMARKS.—This genus and the Australian *Occinirvana* are closely related. The shape of the head differentiates the two genera.

### *Omaranus typicus* Distant
Figs. 277–289

*Omaranus typicus* Distant 1918b: 6. Lectotype ♂, India (BMNH, examined).
*Didius sexualis* Distant 1918b: 36. Lectotype ♀, India (BMNH, examined).

MALE.—Ochraceous (probably green in life). Anterior margin of vertex narrowly black margined, with median, black spot, two smaller, somewhat elongate spots near posterior margin, ocelli black. Dorsal-most area of frontoclypeus and face ventrad of antennal bases, blackish brown, marginal band dorsad of antennal base and longitudinal stripe on proepimeron blackish brown. Apical 0.25 of forewing and stripe along inner margin fuscous. Abdomen with four black stripes; sterna marked with brown stripes. Apical half of hind femora ventrally streaked with brown. A ventral spot near apex of fore femora black.

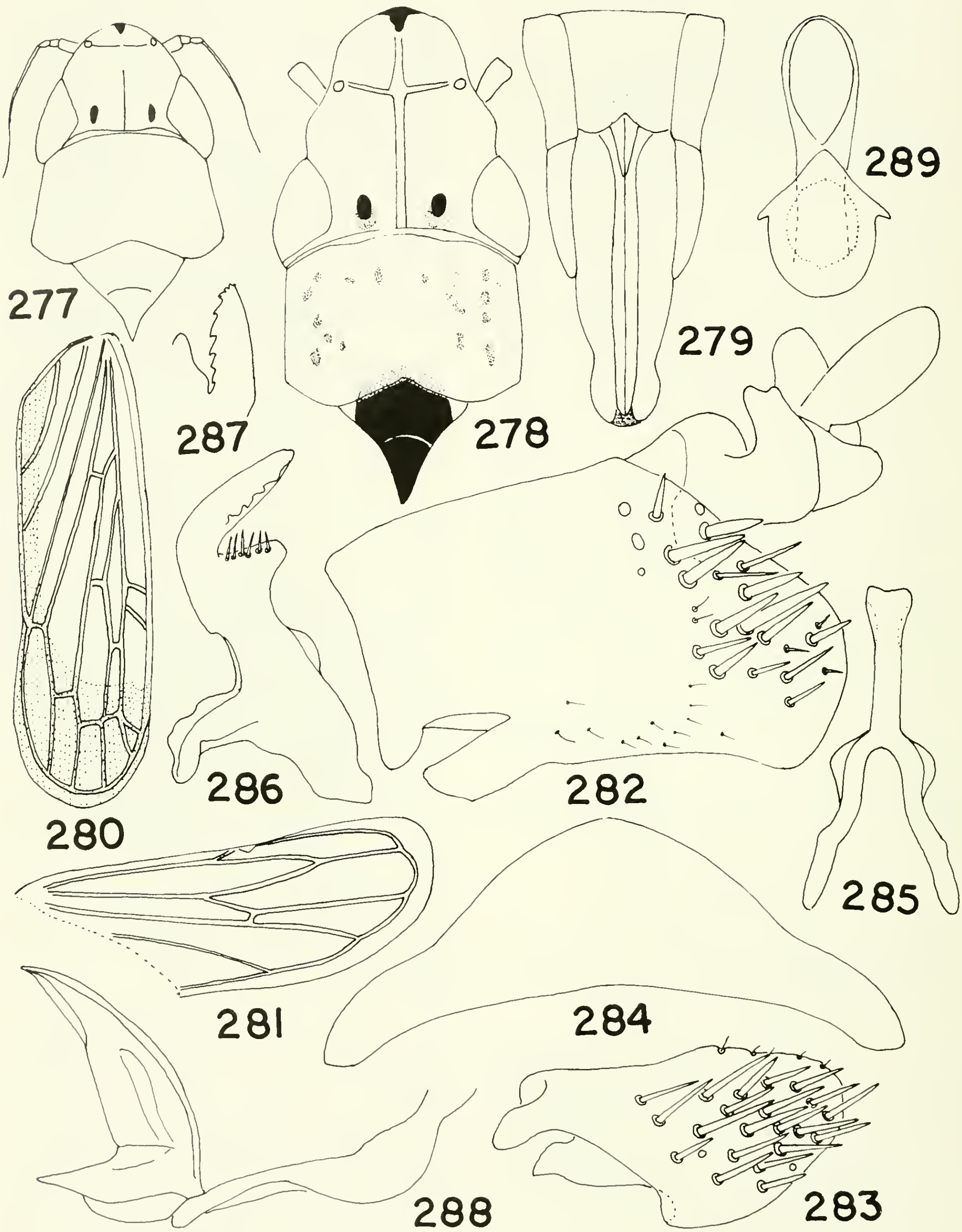
GENITALIA.—Pygofer lobe caudoventrally produced, caudodorsal area beset with stout, short setae. Plate caudally rounded with scattered, stout setae. Valve straplike with caudal margin roundly and medially produced. Apophysis of style curved laterally with series of teeth on lateral margin. Stem of connective 0.75 as long as each arm. Aedeagus with short, dorsal apodeme, shaft stout at base, narrowed caudally in lateral aspect with a large gonopore on dorsal aspect.

FEMALE.—Ochraceous. Head with median spot on anterior margin, ocelli, and two spots near base of vertex black; median stripe, a transverse band across ocelli, hind margin, except medially, and two spots in front of eyes reddish. Dorsal margin of face black from which two apically divergent stripes traverse face. Proepisternum traversed by longitudinal, piceous stripe, much longer on proepisternum; mesopleura and mesocoxae with piceous spot. Pronotum with scattered, dark brown spots, with obscure stripes, two lateral and two median reddish. Scutellum except for two lateral, basal angles in basal half black, apical half blackish brown. Forewing veins marked with red. Fore tibiae and tarsi reddish; fore- and mesothoracic femora black, mesocoxae with piceous spot. Abdominal coloration as in male.

GENITALIA.— Hind margin of seventh sternum with median, U-shaped excavation and translucent in middle. Anal segment concealed by pygofer.

MEASUREMENTS.—Male 4.30 mm long, head 1.00 mm wide, pronotum 1.10 mm wide. Female 7.90 mm long, head 1.00 mm wide, pronotum 1.10 mm wide.

SPECIMENS EXAMINED.—Lectotype ♂ labeled / Calcutta, 28.viii.07, Mus. Coll./ / *Omaranus typicus* Dist., type/ here designated. Paralectotype ♂ labeled / Calcutta, 23.viii.07/ /*Omaranus typicus* Dist., type/ here designated. Paralectotype has the abdomen and left fore and hindwings missing. Lectotype ♀ labeled / Calcutta/ /Distant Coll. 1911–384/ /*Didius sexualis* Dist. type/ here designated (BMNH). India: Punjab: 1 ♂, 1 ♀ nymph, Ludhiana, 13.ix.1966, A. S. Sohi (PAU). India: Madhya Pradesh: 3 ♂, 18 ♀, Nebudda Survey, Sta. No. 31, 37, 58, 21.ii–9.iii.1927, H.S. Pruthi (ZSI).




Figs. 277–289. *Omaranus typicus* Distant: 277, head and thorax of lectotype male; 278, same of lectotype female, *Didius sexualis* Distant; 279, ovipositor; 280, 281, fore and hindwings of male; 282, male pygofer; 283, male plate; 284, male valve; 285, connective; 286, style; 287, 288, aedeagus, lateral and cephalic views.

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# GENUS *FLEXAMIA*: NEW SPECIES, PHYLOGENY, AND ECOLOGY

Robert F. Whitcomb[1] and Andrew L. Hicks[1]

ABSTRACT.—Eight new species of *Flexamia* DeLong are described, and two Mexican species previously synonymized are reinstated. Species are assigned to 13 species groups; keys are presented for the groups and for the 44 recognized species. Host data, in many cases with oligophagy coefficients, are presented for 37 of the species. Many species specialize on native, dominant, perennial, choridoid or panicoid grasses; some are monophagous. Seven sister species pairs specialize on the same (or a closely related) grass species; in addition, four closely related species appear to be restricted to *Bouteloua curtipendula*. Few if any specialists colonize their host throughout its entire range. Ecological factors such as phenology and/or host patchiness strongly influence geographic distribution. An intuitive phylogeny is proposed and is used as a basis for constructing 18 character transformations. The genus *Flexamia* probably originated in Mexico by division of an ancestral lineage from which the modern genus *Spartopyge* also diverged.

The first specimen of the genus *Flexamia* DeLong was apparently collected at Jacksonville, Florida, in the height of the Linnaean explosion; it was deposited in the British Museum (Natural History) and named *Jassus productus* by Walker (1851). In their studies of Iowa prairies in the latter part of the nineteenth century, Osborn and Ball encountered other species, which they referred to the genus *Deltocephalus*. DeLong (1926) erected a subgenus *Flexamia* DeLong within *Deltocephalus* Burmeister. DeLong and Sleesman (1929) recognized that *Deltocephalus* was an unworkably large assemblage of distantly related species and divided the genus into several genera (e.g., *Laevicephalus* DeLong & Sleesman, *Polyamia* DeLong & Sleesman, and *Flexamia*). The genus concept for *Flexamia* was refined by Oman (1949) in his revision of North American cicadellid genera, but the modern generic concept was established by Young and Beirne (1958). These authors segregated *Spartopyge* Young & Beirne, synonymized *Secopennis* Oman, described genitalic characters of males and females (the first use of genitalic characters for *Flexamia* females), and presented a species key. The 30 species they described included all of the widely distributed and commonly collected representatives of the genus, and their key proved to be accurate and easy to use. Young and Beirne also described possible relationships among species and, without specifying an explicit phylogeny, proposed broad outlines of hypothetical evolutionary events in the genus. The genus was incorrectly synonymized with *Acurhinus* Osborn by Linnavuori (1959). Comparison of the specimens (all females) of *Acurhinus* (=*Dorydium*) *maculatum* Osborn in the Ohio State University collection led Linnavuori and DeLong (1978) to synonymize *Acurhinus* with the African stirelline genus *Hododoecus* Jacoli. The genus *Flexamia* as defined herein is an entirely North American taxon related to *Spartopyge*, to *Alapus* DeLong & Sleesman, and, perhaps distantly, to *Aflexia* Oman. The closest Old World relative may be *Enantiocephalus* Haupt.

Although the taxonomic status of *Flexamia* has been generally adequate since 1958, host data have been difficult to obtain. Earlier collectors were not knowledgeable agrostologists and often reported only that deltocephaline species, including *Flexamia*, resided on "grasses." Astute collectors such as Osborn and Ball recognized the importance of biological data, and their notes contain some host records. In 1967, H. H. Ross encouraged the senior author to ascertain the hosts of *Flexamia* species, in large part to test his intuitive belief that host relationships, especially host transfers, could be invoked to explain speciation of phytophagous insects. Accordingly, we sought to determine hosts of the species described by Young and Beirne. Much to our

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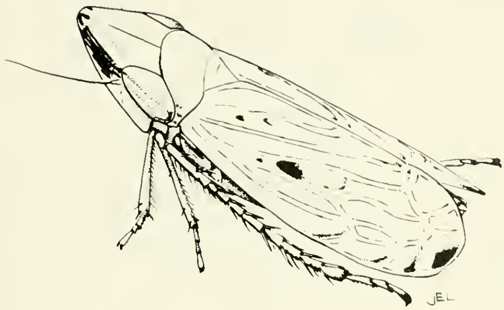


Fig. 1. *Flexamia serrata.*

surprise, in the course of this search, undescribed species emerged, particularly when we examined dominant, perennial *Muhlenbergia* or *Bouteloua* species (Whitcomb et al. 1986, 1987). Under these circumstances, it seems appropriate to review the species concept and to emend the generic concept, which, although basically intact in its essential aspects, must accommodate the new species.

## Genus *Flexamia* DeLong

*Deltocephalus* subgenus *Flexamia* DeLong 1926:20, 22. Type species: *Deltocephalus reflexus* Osborn & Ball 1897, by original designation.
*Flexamius*, DeLong and Sleesman 1929:82.
*Flexamius* subgenus *Secopennis* DeLong & Sleesman 1929:85. Type species: *Deltocephalus slossoni* Ball.
*Acurhinus* Osborn, Linnavuori 1959:89.
*Flexamia* DeLong, Young and Beirne 1958; Linnavuori and DeLong 1978:208.

Small deltocephaline leafhoppers. Length of male 2.4–5.0 mm, of female 2.6–5.0 mm. Head produced, median length of crown usually greater than interocular width; clypellus broader at base than at apex; forewing with reflexed veinlets to costal margin in vicinity of small, outer anteapical cell.

Dried specimens yellowish brown or gray, with ferruginous to black markings; live insects in some cases with green pigmentation changing to orange or stramineous when dried. Apical area of crown partly or completely surrounded by darker markings, in latter case with clearly defined, apical areolet. Crown often with pair of oblique, dark markings at base; pair of transverse, dark markings at about midlength; pair of darker markings parallel to lateral margins near apex. Face color varying from pale to black, often useful in species discrimination. Pronotum of some species with conspicuous, longitudinal stripes, but many species with faint, wider stripes. Veins of forewings usually dark-margined; distinct, dark-margined areole frequently near center of corium.

MALE.—Plates usually shorter than pygofer, frequently fused along mesal margins; pygofer usually with pronounced posterior lobe in lateral aspect; style with longitudinally grooved, preapical lobe, which is usually not pronounced; connective linear, arms contiguous basally, sometimes fused to aedeagus. Connective with upper portion less heavily sclerotized than lower portion, often thinner and extended dorsad in thin keel that varies in width interspecifically; dorsal aedeagal apodeme with pair of conspicuous appendages directed caudoventrad or caudad. Aedeagus interspecifically variable, of great value in species discrimination.

FEMALE.—Sternum VII nearly always longer than VI, often 2X or more; hind margin with 2–4 teeth and usually small, median notch. Pygofer with well-dispersed setae; ovipositor barely reaching pygofer apex.

## *Flexamia* Species Groups

In the following discussion, we describe 13 species groups and provide keys to species. We describe 8 new species and reinstate 2 species previously synonymized. We also review important characteristics of previously described species, emphasizing diagnostic morphology, ecology, and biogeography. Our brief descriptions of previously described species complement the descriptions of Young and Beirne (1958).

### Key to *Flexamia* Species Groups

1. Dorsum with pair of stripes extending from hind portion of disc of crown across pronotum and scutellum (Figs. 2A–D) .................... 2
— Dorsum without such stripes (Figs. 2E,F) ..... 4
2(1). Individuals large, at least 4.5 mm .......... .......................... IV. *grammica* group
— Individuals smaller ........................ 3
3(2). Forewing broadly truncate (Fig. 2D); Arizona .......................... VIII. *ritana* group
— Forewing obliquely truncate (Fig. 2B) or not truncate (Fig. 2A) (prairie); Florida .......... .......................... VII. *albida* group
4(1). Face entirely black, genae at most with oblique, pale streak; crown without midlength transverse lines .................................. 5

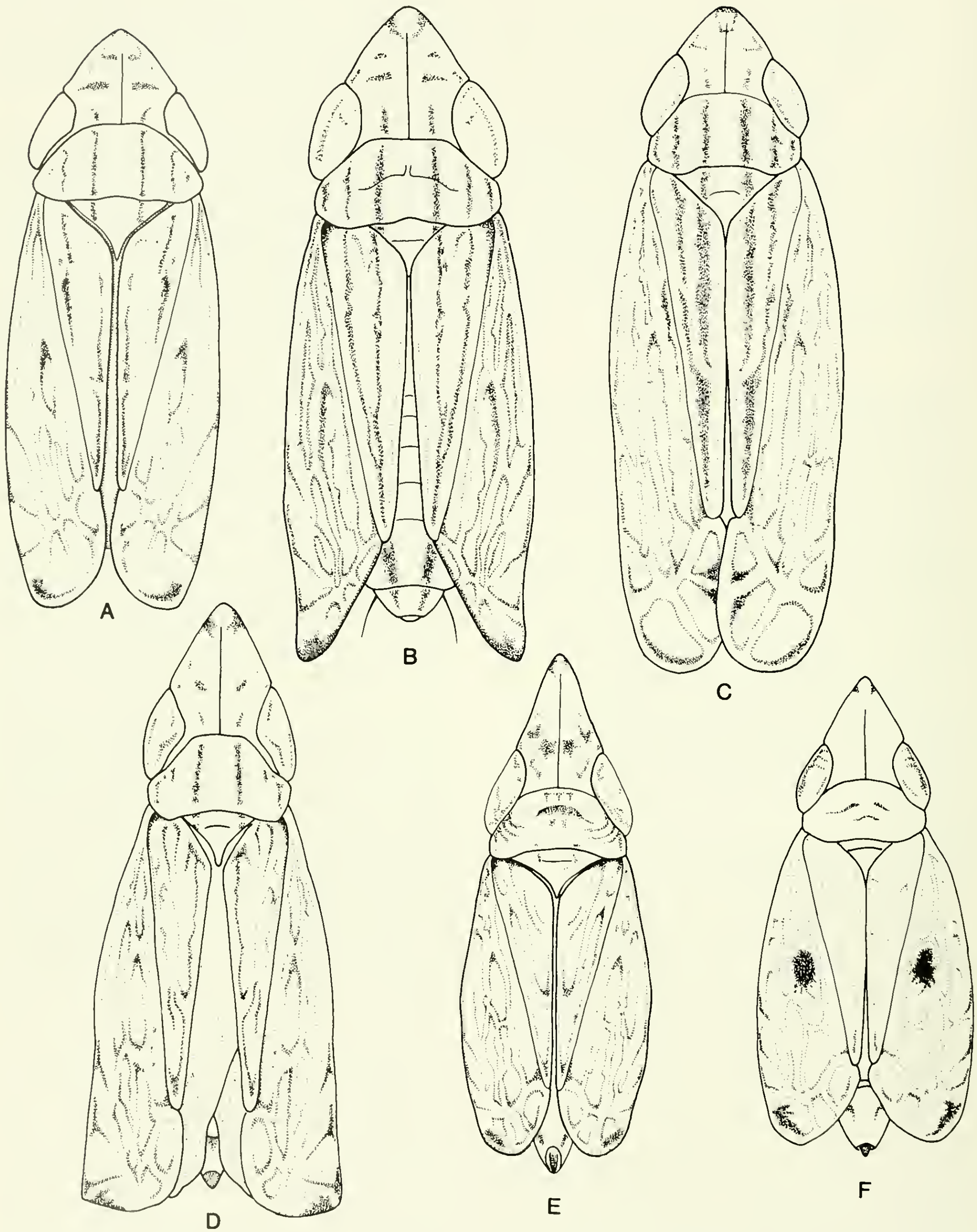


Fig. 2. Habitus of *Flexamia* species: A, *albida;* B, *slossonae;* C, *grammica;* D, *ritana;* E, *pyrops;* F, *areolata.*

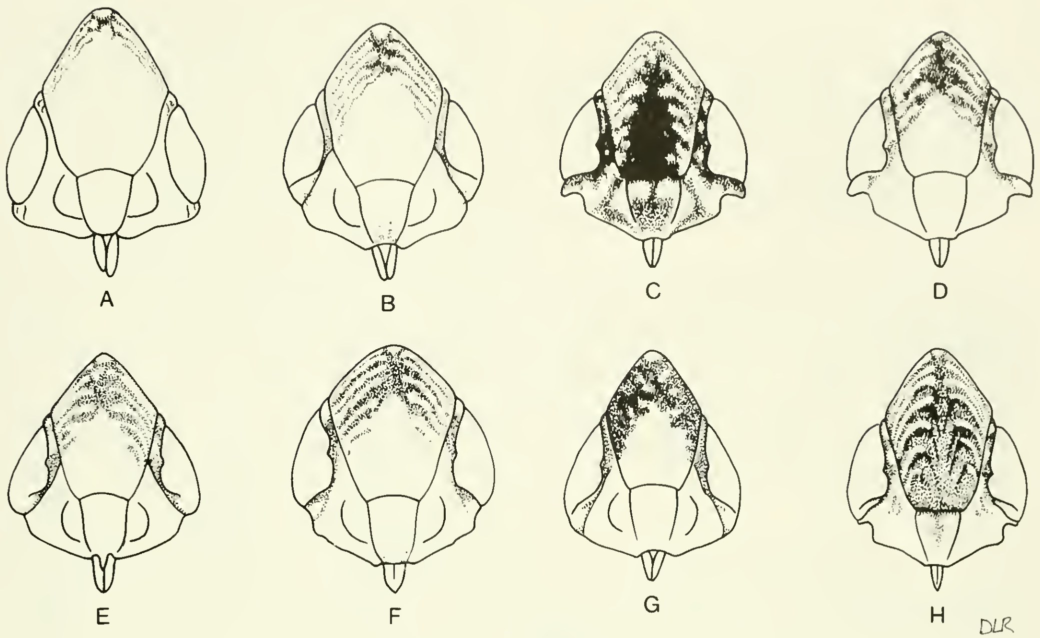


Fig. 3. Faces of *Flexamia* species: A, *serrata;* B, *stylata;* C, *prairiana;* D, *prairiana;* E, *picta;* F, *decora;* G, *flexulosa;* H, *sandersi.*

— Face black basally, pale apically, or brownish in part; at least genae pale, crown usually with midlength transverse lines . . . . . . . . . . . . . . . . . 6

5(4). Forewing with conspicuous black spot (Fig. 2F) in corium; crown with median length more than one-half greater than interocular width . . . . . . . . . . . . . . . . . XII. *areolata* group

— Forewing without conspicuous black spot in corium; crown with median length less than one-half greater than interocular width . . . . . . . . . . . . . . . . . . . . . . . . . . . . . XI. *imputans* group

6(4). Face pale with several narrow, parallel, fuscous, interocular lines interrupted at middle (Fig. 3A); northwestern (Fig. 30) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . XI. *serrata* group

— Face with (Figs. 3B,D–G) or without (Figs. 3C,H) interocular lines but not as above . . . . . 7

7(6). Either with crown more than twice interocular width (Fig. 2E) (*pyrops* Crumb), or with conspicuous, dark, apical wing blotch (Fig. 4C) *and* sordid yellow face with black interocular band (*picta* [Osborn]); viewed laterally, male pygofer with conspicuous, acutely angulate, ventral lobe (Figs. 5A,B); aedeagus (Fig. 6D) with pair of anteapical processes and apical, flangelike processes . . . . . . . VI. *picta* group

Habitus not as above; male pygofer with posterior lobe rounded ventrally; aedeagus not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

8(7). Males . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

— Females . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

9(8). Aedeagus and connective fused (Figs. 6F,G) . . . . . . . . . . . . . . . . . . . . . . XIII. *prairiana* group

— Aedeagus and connective distinctly articulated (Figs. 6A–C, E) . . . . . . . . . . . . . . . . . . . 10

10(9). Aedeagus without apical processes (Fig. 6C) 11

— Aedeagus with (at least minute) apical . . . . . . processes . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

11(10). Male plates broad, not tapered (Figs. 11A–I) . . . . . . . . . . . . . . . . . . . . . . . . . . . I. *pectinata* group

— Male plates more elongate and tapered (Figs. 9C,F) . . . . . . . . . . . . . . . . . . . . III. *zacate* group

12(10). Aedeagus (Figs. 7F,G) with 2 pairs of processes . . . . . . . . . . . . . . . . . . . . V. *curvata* group

— Aedeagus not so . . . . . . . . . . . . . . . . . . . . . . . 13

13(12). Aedeagus with 2 processes on shaft (Fig. 7H) . . . . . . . . . . . . . . . . . . . . . . . .II. *abbreviata* group

— Aedeagus with 3 processes on shaft (Figs. 6E, 31A,D–M) . . . . . . . . . . . . . . . X. *flexulosa* group

14(8). Face white, ivory, or very pale yellow, sharply contrasting with black interocular line (Figs. 3B,F,G) . . . . . X. *flexulosa* group (in part)

— Face with lower part not white or pale (Fig. 3H), or if pale, not contrasting sharply with interocular band, or interocular band brown, not black (Fig. 3D) . . . . . . . . . . . . . . . . . . . . 15

15(14). Body color stramineous . . . . . . . . . . . . . . . . 16

— Body color not stramineous . . . . . . . . . . . . . 17

16(15). Hind margin of sternum VII with medial projection (Fig. 10O) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .X. *flexulosa* group (*inflata* subgroup)

— Hind margin of sternum VII without projection . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 20

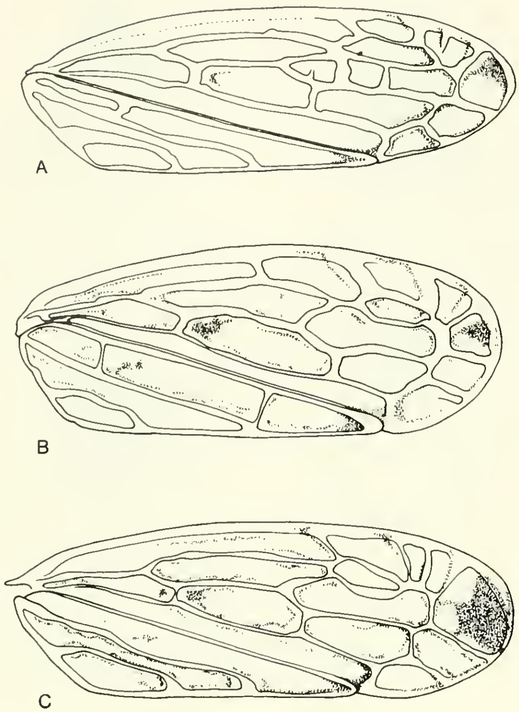


Fig. 4. Wings of *Flexamia* species: A, *inflata;* B, *curvata;* C, *picta.*

17(15). Sternum VII (Fig. 10E) with median, trapezoidal projection, with a medial notch, usually with smaller, shallower notches on either side . . . . . . . . . . . . . . . . . . . II. *abbreviata* group

— Sternum VII not as above . . . . . . . . . . . . . . . . 18

18(17). Sternum VII produced medially in a distinct lobe or projection (Figs. 10S,T) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .XIII. *prairiana* group

— Sternum VII not produced medially in distinct lobe, or if produced, with deep, median incision . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 19

19(18). Hind margin of sternum VII incised to form pattern of four teeth; hind margin usually heavily infuscated on hind margin in vicinity of teeth (Figs. 14A–H) . . . . . I. *pectinata* group

— Hind margin of sternum VII not so . . . . . . . . 20

20(19). Hind margin of sternum VII slightly concave on each side of median excision; infuscated notches usually contrasting sharply with stramineous color of sternum (Figs. 10J,K) . . . . . . . . . . . . . . . . . . . . . . . . . V. *curvata* group

— Hind margin of sternum VII not so (Figs. 10I,L) . . . . . . . . . . . . . . . . . . . . III. *zacate* group

## I. The *pectinata* Group

The greatest proposed changes in *Flexamia* species concepts are in the *pectinata* species group to which we add five new species and reinstate two others. All species of the group have aedeagal shafts without apical processes. Although aedeagal characters are not as useful for species discrimination in this group as in other groups, the male plates and female sternum VII provide useful apomorphies that define the group. The plates (except in *collorum*) are broad and basally parallel-sided. The hind margins of the female sternum VII of all species possess four medial teeth with surrounding infuscation (but note the extensive modification in *mescalero* [Fig. 21H]). The size and shape of the teeth vary interspecifically. The species are largely southwestern and/or Mexican, and many appear to have small ranges. The nominate species *F. pectinata*, however, has a wide geographic range. As defined by Young and Beirne (1958), this species ranges from western Mexico (*zamora* DeLong & Hershberger) through the eastern highlands (Valles and Monterrey [*minima* DeLong & Hershberger]), the Davis Mountains of west Texas, Otero and Guadalupe counties of New Mexico north to North Dakota, and as far east as Akron, Ohio, in the prairie peninsula. However, our studies indicate that *zamora* and *minima* should be reinstated. Recognition herein of the new species *bandarita, gila, collorum, jacala,* and *mescalero* makes it clear that this group is diverse and has speciated frequently. The host of *pectinata* is side-oats grama (*Bouteloua curtipendula*), a widespread prairie species. In addition to *pectinata*, there are three southwestern side-oats grama specialists of the *pectinata* group. *Flexamia doeringae* and *F. gila* reside in the southeastern Arizona mountains and Mogollon Rim region and extended conifer-oak savanna of Mexico, respectively. *Flexamia bandarita*, as far as known, is confined to the Chisos Mountains and Marathon Basin of Trans-Pecos Texas. We suspect that side-oats grama, which also has a wide range in Mexico, will prove to be the host of some Mexican species of the *pectinata* group. The most distinctive species of the group (*mescalero*), however, appears to specialize on *Muhlenbergia pauciflora.*

Several factors may account for speciation in the *pectinata* group. Side-oats grama is itself a complex of ecotypes that vary greatly in structure and seasonality (Gould 1979). This

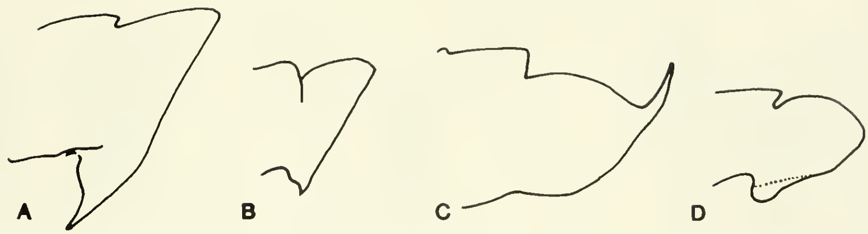


Fig. 5. Pygofers of *Flexamia* species: A, *picta;* B, *pyrops;* C, *stylata;* D, *producta.* Redrawn from Young and Beirne (1958).

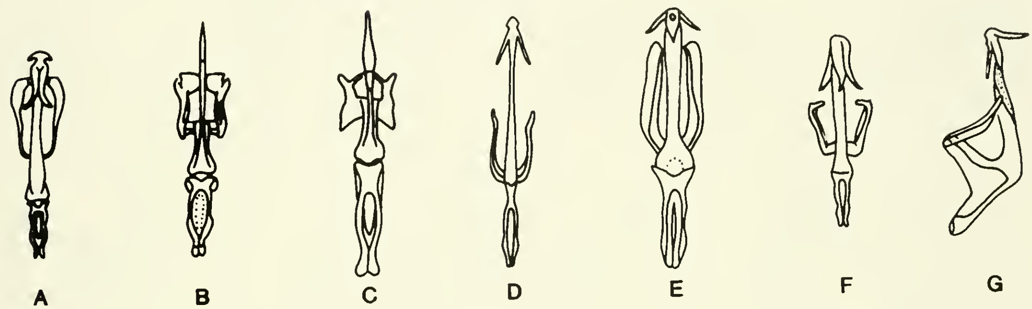


Fig. 6. Aedeagus and connective of *Flexamia* species: A, *curvata;* B, *abbreviata;* C, *canyonensis;* D, *picta;* E, *flexulosa;* F, *prairiana;* G, *graminea.* Redrawn from Young and Beirne (1958). Aspects: A-F, caudoventral; G, lateral.

chloridoid grass crosses many biome lines and is a dominant in mesic Sonoran and Chihuahuan grasslands and in montane systems within these semiarid grasslands. It is common through much of the prairie and occurs eastward on nonforested slopes in the Appalachian mountains. Like other major dominants of North American grasslands, therefore, side-oats grama has a much wider geographic range than any of the cicadellid species that exploit it.

The Chihuahuan desert system presents a major barrier to geographical continuity of prairie grasses, and side-oats grama is no exception. Many prairie cicadellid taxa occur west of this desert system, but, depending upon the case, the taxonomic results vary. For example, populations related to the buffalograss specialist *Athysanella* (*Gladionura*) *emarginata* occur in disjunct stands of *Buchloë* in New Mexico's Hidalgo County. This population, until very recently, had been regarded as a subspecies (*sobrina*) but will be elevated to a species in a forthcoming revision of *Gladionura* (H. D. Blocker, personal communication). On the other hand, forms of *A. (Gladionura) argenteola* (a *Bouteloua gracilis* specialist) in southeastern Arizona are not distinguishable from short-grass prairie forms. The connecting link between the relatively mesic, temperate grasslands of the northern Mexican highlands and the prairie is tenuous at best, consisting of a small set of "stepping stone" montane islands within the Chihuahuan desert of Coahuila and Chihuahua, or of the relatively narrow grassland periphery surrounding the desert on the east and west and meeting at the south in the state of San Luis Potosí. Also, the mesquite-acacia savanna and Trans-Pecos shrub savanna of Texas are further barriers to geographic continuity of *B. curtipendula.* During full glaciations, these arid regions had climates that were much more moist than they are today (Van Devender and Burgess 1985).

One of the new species, *collorum*, from the Edwards Plateau of central Texas, is apparently a specialist on Nealley grama, *Bouteloua*

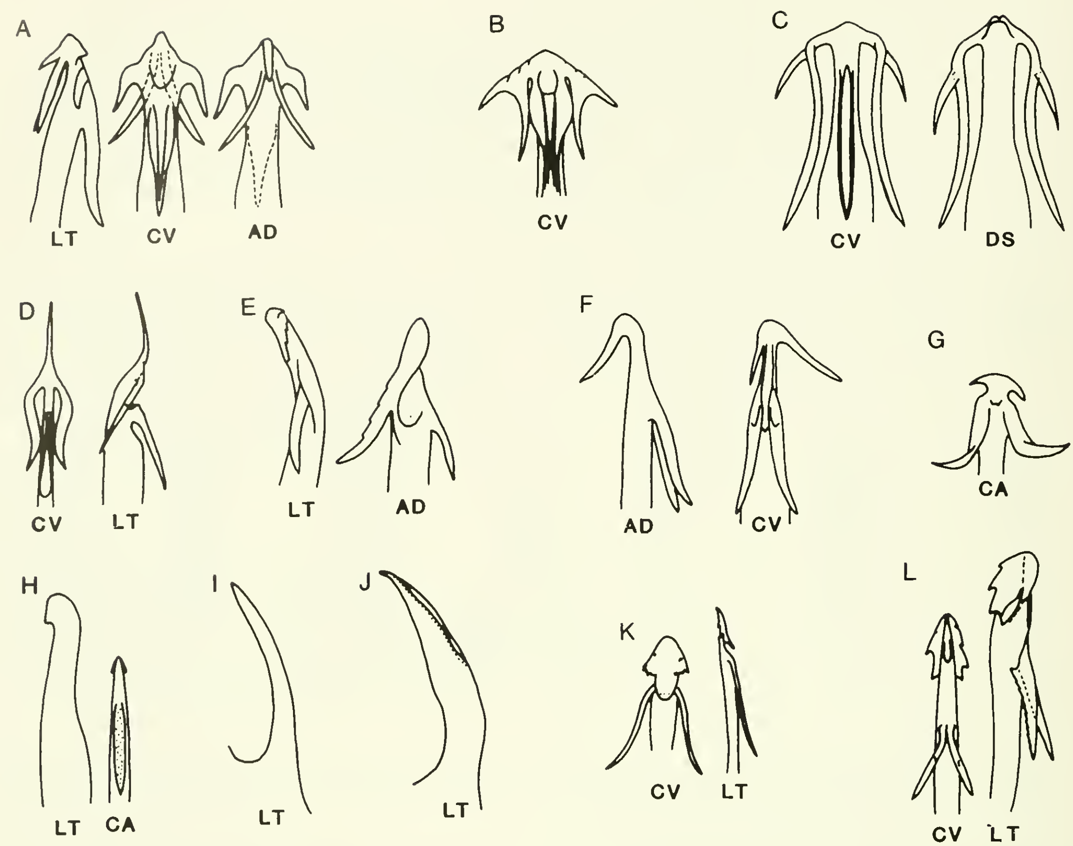


Fig. 7. Aedeagal apices of *Flexamia* species: A, *serrata;* B, *albida;* C, *slossonae;* D, *ritana;* E, *grammica;* F, *curvata;* G, *surcula;* H, *abbreviata;* I, *zacate;* J, *canyonensis;* K, *picta;* L, *pyrops*. Aspects: AD, anterodorsal; CA, caudal; CV, caudoventral; DS, dorsal; LT, lateral. Redrawn from Young and Beirne (1958).

*uniflora*. *Flexamia collorum* may be related to another new species, *jacala*, whose type locality in Mexico is close to the intersection of eastern and western montane Mexican grasslands. The latter species is represented by a single male specimen from the USNM, so nothing is known about its biology.

Finally, another new species, *mescalero*, discovered in a single location in southeastern New Mexico, presumably arose by host transfer to New Mexican muhly, *Muhlenbergia pauciflora*.

## Description of the *pectinata* Group

Medium-sized to small deltocephaline leafhoppers. Length of ♂ 2.7–3.8 mm, of ♀ 2.8–4.2 mm. Species with general facies of genus; brown or in dark specimens, almost black. Crown variably produced. [♂] Plates (Figs. 11A–I) elongate, broad, parallel-sided basally (except *collorum*). Pygofer with distinct, posterior lobe, strongly constricted in lateral aspect, both dorsally and ventrally. Aedeagus and connective distinctly articulated. Aedeagus (Figs. 12A–I) with no apical processes, or at most slightly capitate (*mescalero*), often appearing flared in dorsal aspect. [Note: Caution must be exercised when using the aedeagal apex as a diagnostic character, since this structure is membranous and is subject to tearing and breaking during copulation or preparation of the specimen.] Styles variable interspecifically (Figs. 13A–I). Gonopore subapical on caudoventral surface. [♀] Sternum VII (Figs. 14A–H) with four medial teeth on hind margin; teeth varying interspecifically in length and shape, surrounded by infuscated region.

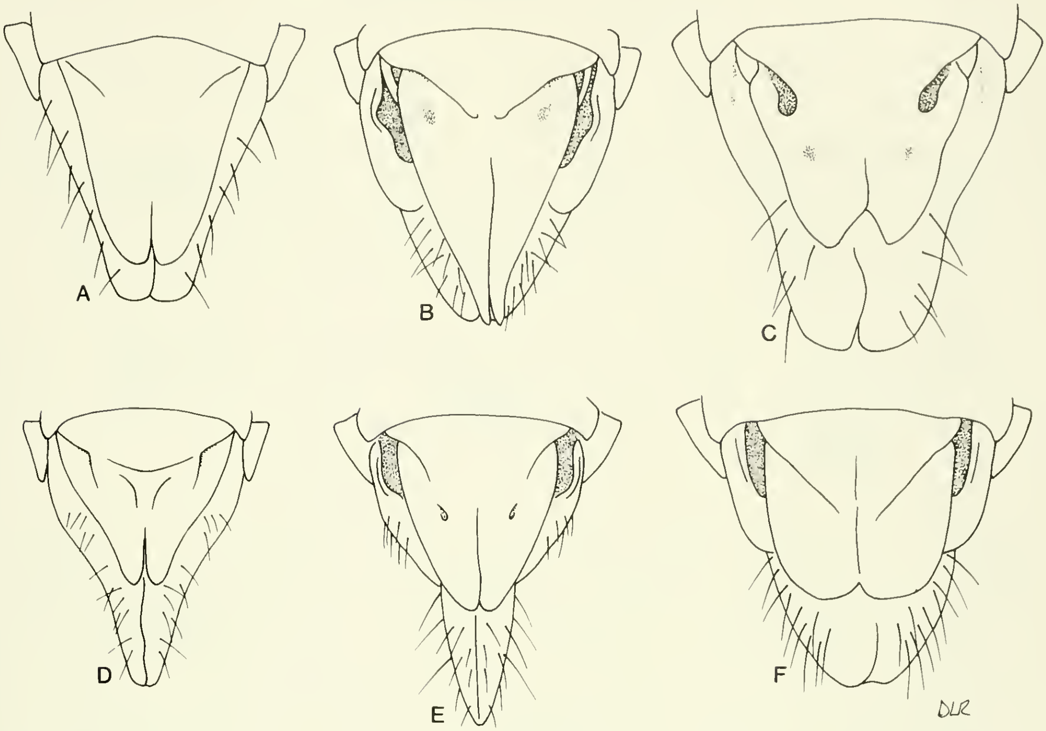


Fig. 8. Male plates and pygofers of *Flexamia* species: A, *albida*; B, *slossonae*; C, *serrata*; D, *ritana*; E, *abbreviata*; F, *grammica*.

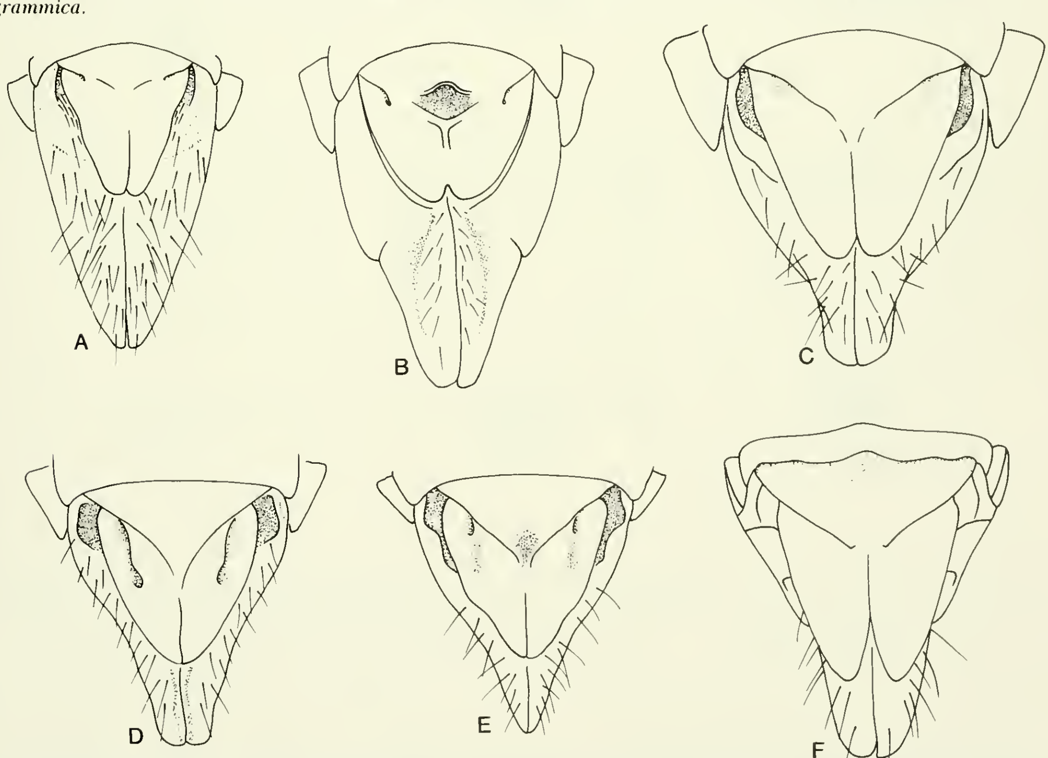


Fig. 9. Male plates and pygofers of *Flexamia* species: A, *picta*; B, *pyrops*; C, *canyonensis*; D, *curvata*; E, *surcula*; F, *zacate*.

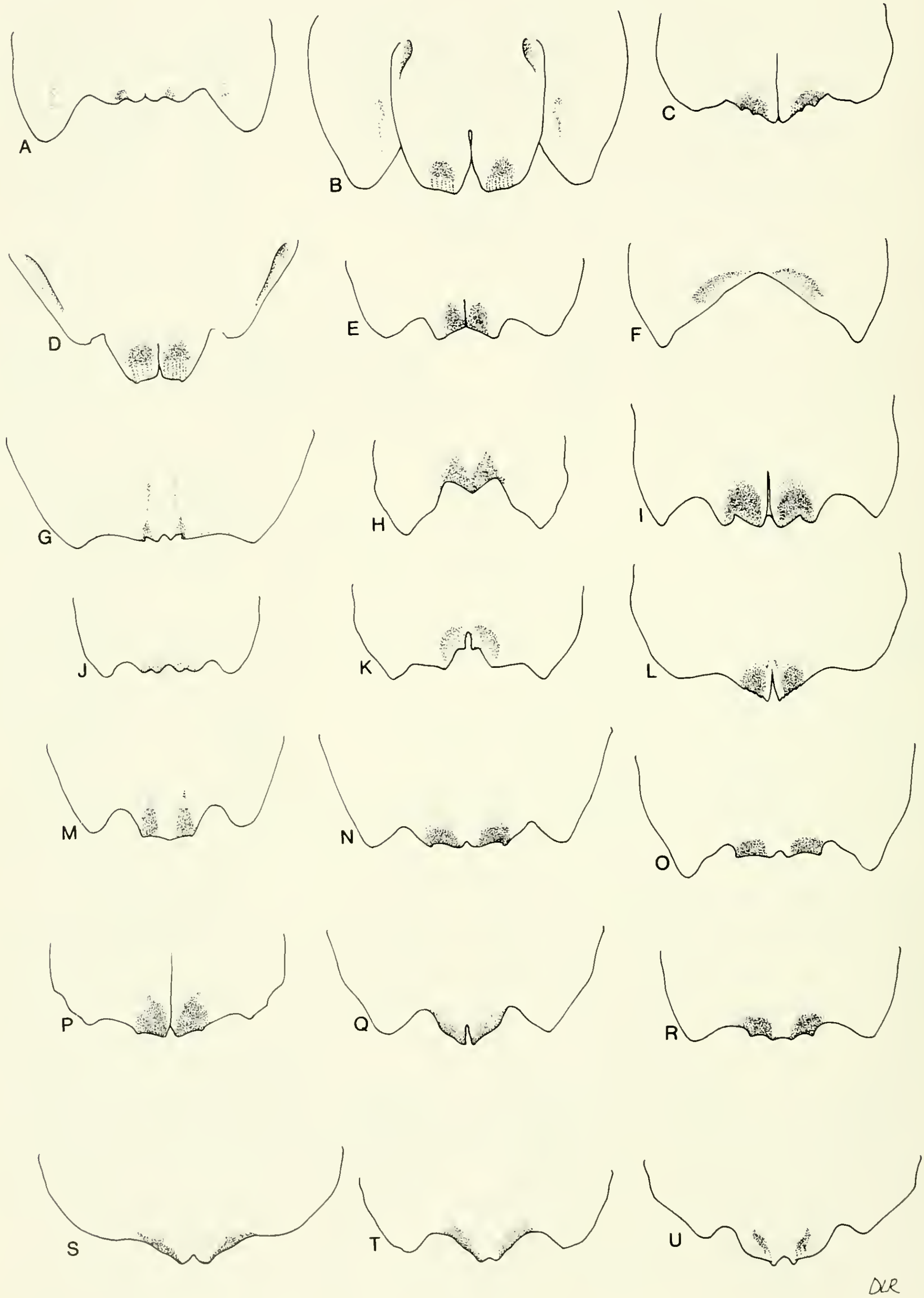


Fig. 10. Female sternum VII of *Flexamia* species: A, *albida;* B, *slossonae;* C, *serrata;* D, *ritana;* E, *abbreviata;* F, *grammica;* G, *picta;* H, *pyrops;* I, *canyonensis;* J, *surcula;* K, *curvata;* L, *zacate;* M, *flexulosa;* N, *decora;* O, *inflata;* P, *imputans;* Q, *areolata;* R, *stylata;* S, *prairiana;* T, *sandersi;* U, *graminea.*

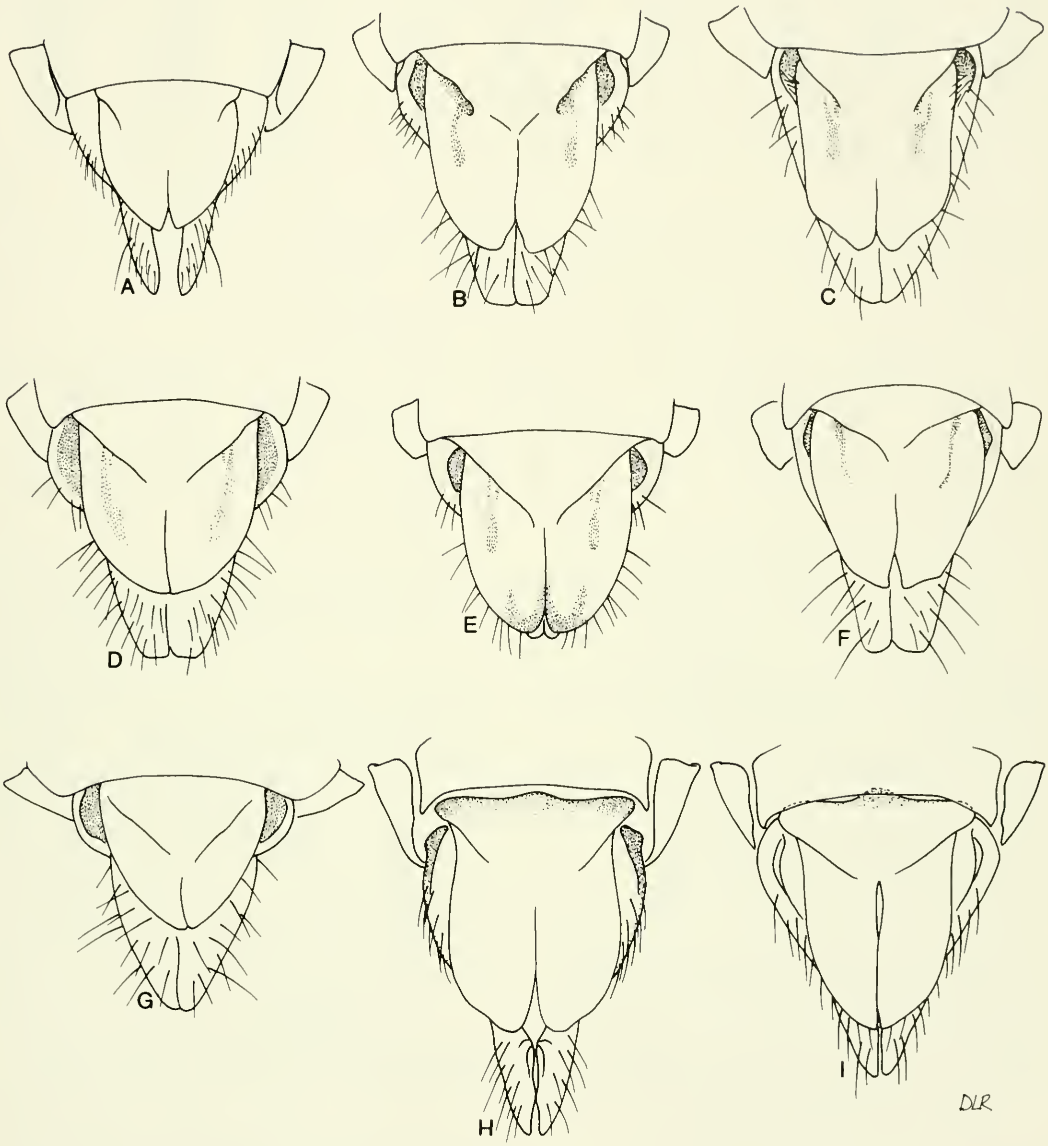


Fig. 11. Male plates and pygofers of *Flexamia pectinata* group, ventral aspect: A, *minima;* B, *zamora;* C, *pectinata;* D, *bandarita;* E, *gila;* F, *doeringae;* G, *collorum;* H, *jacala;* I, *mescalero.*

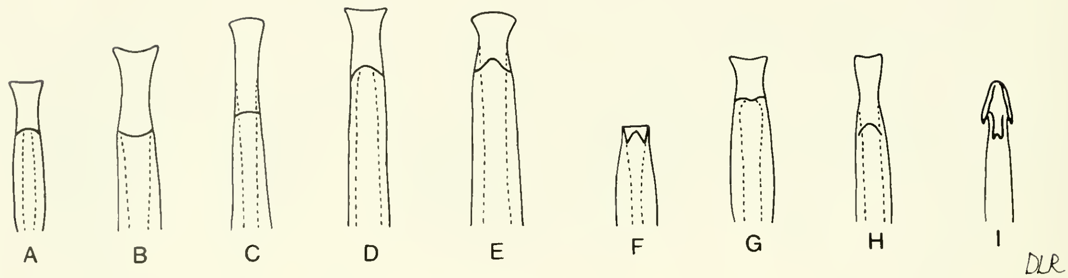


Fig. 12. Aedeagal apices of *Flexamia pectinata* group, caudoventral aspect: A, *minima;* B, *zamora;* C, *pectinata;* D, *bandarita; E, gila;* F, *doeringae;* G, *collorum;* H, *jacala;* I, *mescalero.*

Key to Males of the *pectinata* Group

1. Plates long and parallel-sided at bases . . . . . . . . . 2
— Plates short, not parallel-sided . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *collorum* Whitcomb & Hicks
2(1). Plates subrectangular (Figs. 11C,F) . . . . . . . . . . 3
— Plates with apices rounded . . . . . . . . . . . . . . . . . . 4
3(2). Aedeagus in ventral aspect (Fig. 12F) with protuberance close to tip; face pale; Arizona . . . . . . . . . . . . . . . . . . . . . . . . . *doeringae* Beamer & Tuthill
— Aedeagus in ventral aspect with protuberance considerably removed from tip (Fig. 12C); face brown; prairie . . . . . . . . *pectinata* (Osborn & Ball)
4(2). Plates (Fig. 11A) with apices acute; Mexico . . . . . . . . . . . . . . . . . . . *minima* DeLong & Hershberger
— Plates with apices not acute . . . . . . . . . . . . . . . . . 5
5(4). Plates almost as long as pygofer (Fig. 11E) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *gila*, n. sp.
— Plates no more than 3/4 length of pygofer . . . . . . 6
6(5). Aedeagus expanded apically in ventral aspect, appearing bluntly saggitate (Figs. 12I, 22) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *mescalero*, n. sp.
— Aedeagus not expanded apically . . . . . . . . . . . . . 7
7(6). Style apex (Fig. 13H) avicephaliform in lateral aspect . . . . . . . . . . . . . . . . . . . . . . . . . . *jacala*, n. sp.
— Style apex not avicephaliform . . . . . . . . . . . . . . . 8
8(7). Style apex (Fig. 13D) ventrally directed, chelate . . . . . . . . . . . . . . . . . . . . . . . . . . . *bandarita*, n. sp.
— Style apex (Fig. 13B) not chelate . . . . . . . . . . . . . . . . . . . . . . . . . . . *zamora* DeLong & Hershberger

Key to Females of the *pectinata* Group

1. Sternum VII with 4 teeth of approximately equal length and 3 relatively shallow incisions . . . . . . . 2
— Sternum VII with deep incisions and/or teeth of different length . . . . . . . . . . . . . . . . . . . . . . . . . . 4
2(1). Sternum VII with infuscations on either side of middle incision (Fig. 14G); Texas, host *Bouteloua uniflora* . . . . . . . . . . . . . . . . . . *collorum*, n. sp.
— Sternum VII not as above . . . . . . . . . . . . . . . . . . 3
3(2). Sternum VII with heavy infuscation around teeth on hind margin (Fig. 14C); USA, prairie . . . . . . . . . . . . . . . . . . . . . *pectinata* (Osborn & Ball)
— Sternum VII with light infuscation on hind margin (Fig. 14A); Mexico . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *minima* DeLong & Hershberger
4(1). Sternum VII with outer teeth longer than inner teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
— Sternum VII with inner teeth longer than outer teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
5(4). Sternum VII with outer teeth sharply pointed, median incision shallow (Fig. 14B); Mexico . . . . . . . . . . . . . . . . . . . *zamora* DeLong & Hershberger
— Sternum VII with outer teeth blunt, median incision deep (Fig. 14H) . . . . . . . *mescalero*, n. sp.
6(4). Inner teeth of sternum VII together forming blunt, median projection (Fig. 14F) . . . . . . . . . . . . . . . . . . . . . . . . . . *doeringae* Beamer & Tuthill
— Inner teeth of sternum VII separated, acute at tip, separated by tapered incision . . . . . . . . . . . . 7
7(6). Sternum VII with three incisions of equal depth (Fig. 14E) . . . . . . . . . . . . . . . . . . . . . . . . *gila*, n. sp.
— Sternum VII with median incision deeper than lateral incisions (Fig. 14D) . . . . . *bandarita*, n. sp.

## 1. *Flexamia minima* DeLong & Hershberger, n. stat.

*Flexamia minima* DeLong & Hershberger 1947: 138.
*Flexamia pectinata*, Young & Beirne 1958: 46. (In part.)

Length of ♂ 2.9 (2.8–2.9) mm, ♀ 3.0 (2.7–3.2) mm; head width of ♂ 0.84 mm, ♀ 0.92 mm. Crown produced; median length of crown 0.74 x head width and 1.45 x interocular width (♂ n = 6; ♀ n = 3). Crown light brown to pale yellow with dark, circular spot around apex, pair of broken, transverse lines at midlength, two oblique markings at rear, appearing continuous with the medial pair of six pale brown, pronotal stripes. Face with broad, dark brown, interocular band, fading to pale yellowish. Brown basally, disc and

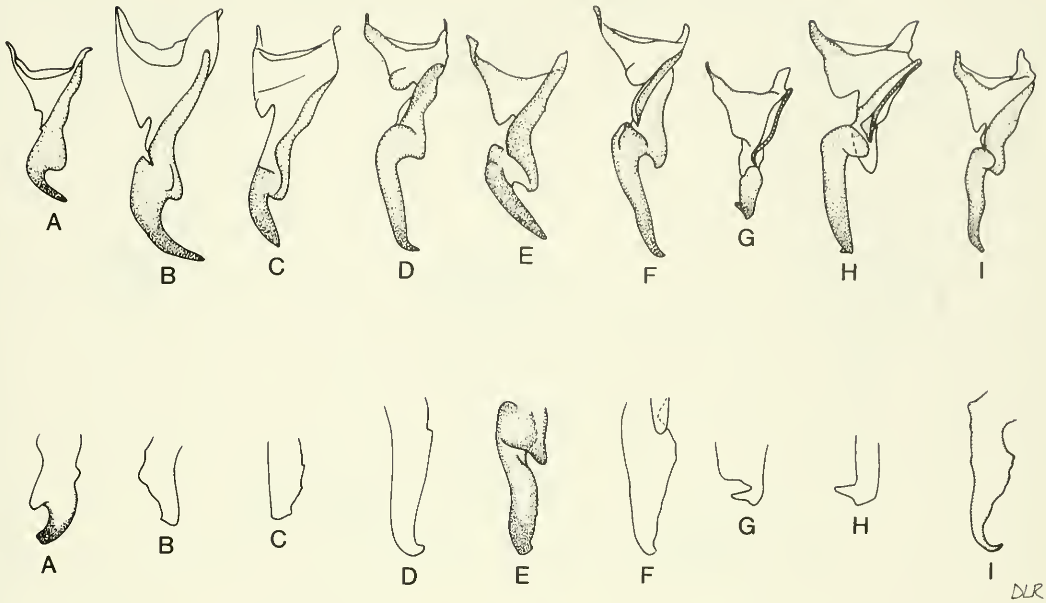


Fig. 13. Styles and style tips of *Flexamia pectinata* group: A, *minima;* B, *zamora;* C, *pectinata;* D, *bandarita;* E, *gila;* F, *doeringae;* G, *collorum;* H, *jacala;* I, *mescalero.*

apex of forewings usually with irregular, dark spot.

MALE.—Pygofer much like that of *pectinata* but shorter; plates (Fig. 11A) barely exceeding ventral lobe in lateral view or 2/3 length of pygofer, unevenly tapering to blunt apices. Genitalia similar to those of *pectinata* and *zamora*, but little more than half their size. In ventral aspect, apex of style not exceeding plane of well-developed, preapical lobe, angle formed between preapical lobe and style apex more acute than in *pectinata*. Connective similar to that of *pectinata*, but with a narrower, deeper, U-shaped incision at the joint with the aedeagus. Other characters as in *pectinata*.

FEMALE.—Sternum VII with posterior margin broadly, shallowly emarginate, hind margin with four teeth of approximately equal length (Fig. 14A), lightly infuscated. Ovipositor with bases of first valvulae as in *zamora*.

TYPES.—Holotype ♂: Valles, San Luis Potosí, Mexico, 1 December 1938, J. S. Caldwell.

REMARKS.—An additional series of *minima*, collected by E. D. Ball at Monterrey, Nuevo León (5♂, 3♀, 11 August 1936, USNM), has been examined. On the basis of characters of the male plates, the styles, and the distinctiveness of the female sternum VII from that of *zamora*, we reinstate *minima*. Species problems in this group are discussed under "Species Concept." This species, like *zamora*, may be entirely Mexican in distribution and is represented by the two collections discussed above (Fig. 15). The host or hosts are unknown, but the closely related *pectinata* specializes on *Bouteloua curtipendula*. The grasslands of San Luis Potosí are extensive, and many other warm season grasses, including other *Bouteloua* spp., are present (Rzedowski 1966); further fieldwork is required to clarify the biology of *minima*.

### 2. *Flexamia zamora* DeLong & Hershberger, n. stat.

*Flexamia zamora* DeLong and Hershberger 1947: 137.
*Flexamia pectinata*, Young and Beirne 1958: 46. (In part.)

Length of ♂ 3.6 (3.5–3.7) mm, ♀ 3.9 (3.7–4.2) mm; head width of ♂ 1.08 mm, ♀ 1.15 mm. Crown not strongly produced; median length of crown 0.61 x head width and 1.27 x interocular width (♂ n = 7; ♀ n = 3).

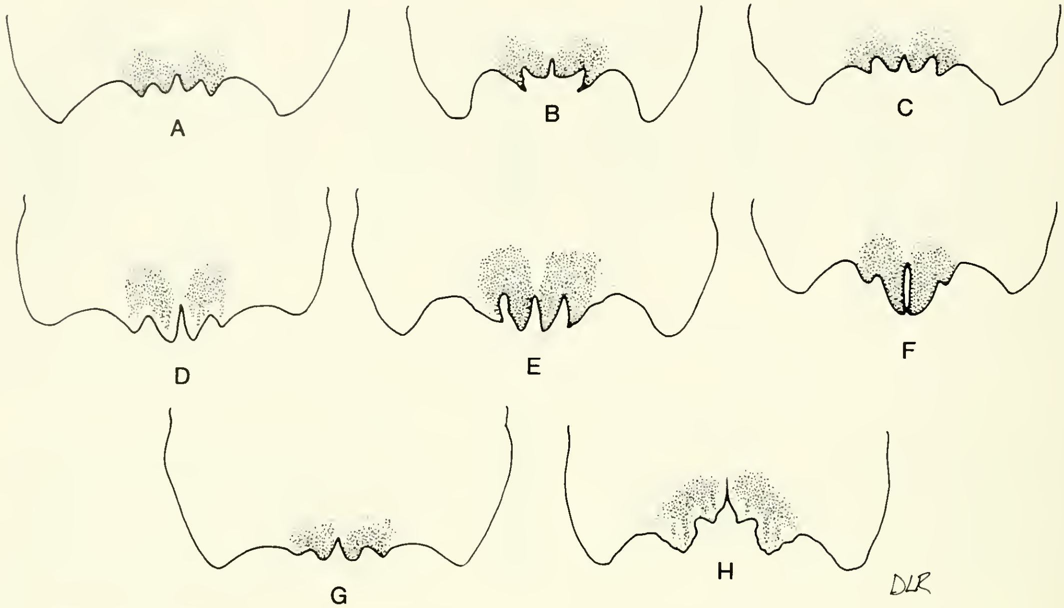


Fig. 14. Female sternum VII of *Flexamia pectinata* group: A, *minima;* B, *zamora;* C, *pectinata;* D, *bandarita;* E, *gila;* F, *doeringae;* G, *collorum;* H, *mescalero.*

Crown light brown with dark, circular spot around apex, pale brown, transverse line on either side at middle. Pronotum light brown, usually with traces of four wide longitudinal stripes. Elytra subhyaline, dark brown spot on disc; costal veinlets heavily margined with dark brown. Face black above, pale brown on lower portion.

MALE.—Pygofer as in *pectinata.* Plates (Fig. 11B) extending to approximately 3/4 length of pygofer, with apices less produced than in *pectinata*, bluntly rounded. Style apices exceeding the plane of the moderately developed, preapical lobe, forming an angle with it smaller than that in *pectinata.* Other characters as in *pectinata.*

FEMALE.—Sternum VII (Fig. 14B) with posterior margin shallowly emarginate; four produced teeth at middle; outer teeth longer, acute, curved inward. Ovipositor with basal processes of first valvulae similar to those of *pectinata*, but recurved portion not separated along the middle.

TYPES.—Holotype ♂: Zamora, Michoacán, Mexico, 2 October 1941, Plummer, Good, Caldwell and DeLong (OSU). Paratypes: 5 ♂, 3 ♀, same collection data (OSU and USNM).

REMARKS.—Although the male genitalia of *zamora* are similar to those of *pectinata*, the styles of *zamora* differ in having a more acute angle between the apex and the less well-developed preapical lobe. Also, the plates are more evenly rounded than those of *pectinata* and longer than those of *minima.* The female sternum VII of *zamora* differs from that of *pectinata* in that the outer teeth of the hind margin are much longer than the inner teeth; in *pectinata* and *minima* the teeth are of equal length. This species, almost certainly entirely Mexican in distribution, is known only from its type locality (Fig. 15). The host or hosts are unknown, but other members of the complex feed on *Bouteloua curtipendula.*

### 3. *Flexamia pectinata* (Osborn & Ball)

*Deltocephalus pectinatus* Osborn & Ball 1897: 205.
*Deltocephalus (Flexamia) pectinatus* DeLong 1926: 32.
*Flexamius pectinatus*, DeLong and Sleesman 1929: 83.
*Flexamius zamora*, Young and Beirne 1958: 46. Incorrect synonymy.
*Flexamia minima*, Young and Beirne 1958: 46. Incorrect synonymy.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (2.9–3.8), of ♀ 3.6 (3.1–4.0). Head slightly produced (median crown length 1.40 x interocular width; 0.62 x head width) (♂ n = 37;

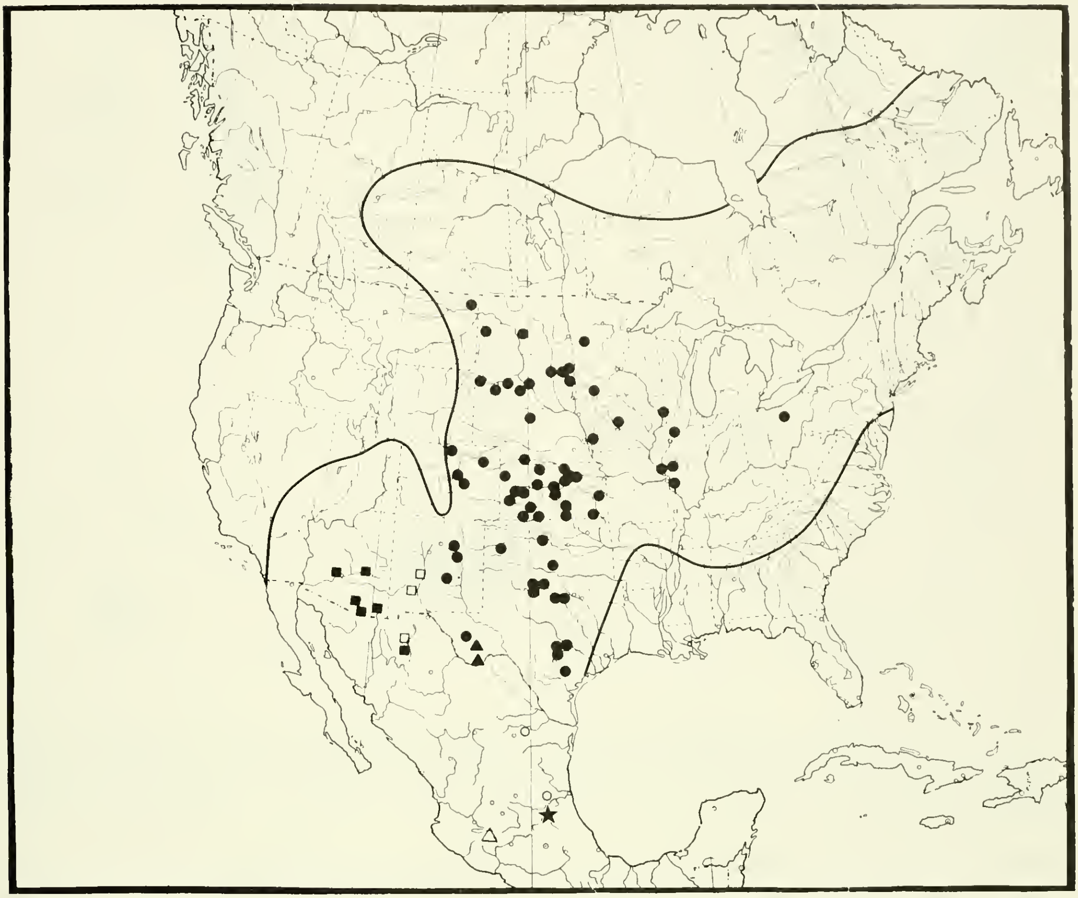

Fig. 15. Geographic distribution of *Flexamia pectinata* (●), *doeringae* (■), *bandarita* (▲), *gila* (□), *zamora* (△), *minima* (○), and *jacala* (★) with *Bouteloua curtipendula*.

♀ n = 29). [♂] Pygofer (Fig. 62F) strongly constricted both ventrally and dorsally; plates (Fig. 11C) wide and parallel-sided for much of their length, almost subrectangular, but with rounded tips. Aedeagus (Fig. 12C) symmetrical, without lateral processes; gonopore subapical on caudoventral surface. [♀] Sternum VII (Fig. 14C) with four teeth of approximately equal length. Ovipositor with bases of first valvulae recurved and calipterate (Fig. 63G).

GEOGRAPHIC DISTRIBUTION.—This species is a specialist of side-oats grama (*Bouteloua curtipendula*) in prairie and mesic grasslands; it occurs (Fig. 15) at higher elevations of the desert plains of eastern New Mexico east to Akron, Ohio, the eastern extension of the prairie peninsula (Transeau 1935).

BIOLOGY.—Like other *Flexamia* species, *pectinata* is probably multivoltine and is present throughout the growing season. In New Mexico it is often absent from its host (*Bouteloua curtipendula*, side-oats grama) at lower elevations where host growth may be unpredictable because of sporadic drought. In Chihuahuan and Sonoran highlands it is replaced by *bandarita* and *doeringae*, respectively, and in the intervening mountains, by *gila*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.973; *Bouteloua* 0.926; *Bouteloua curtipendula* 0.825 (n = 57).

REMARKS AND DIAGNOSIS.—*Flexamia pectinata* can be recognized by a combination of its

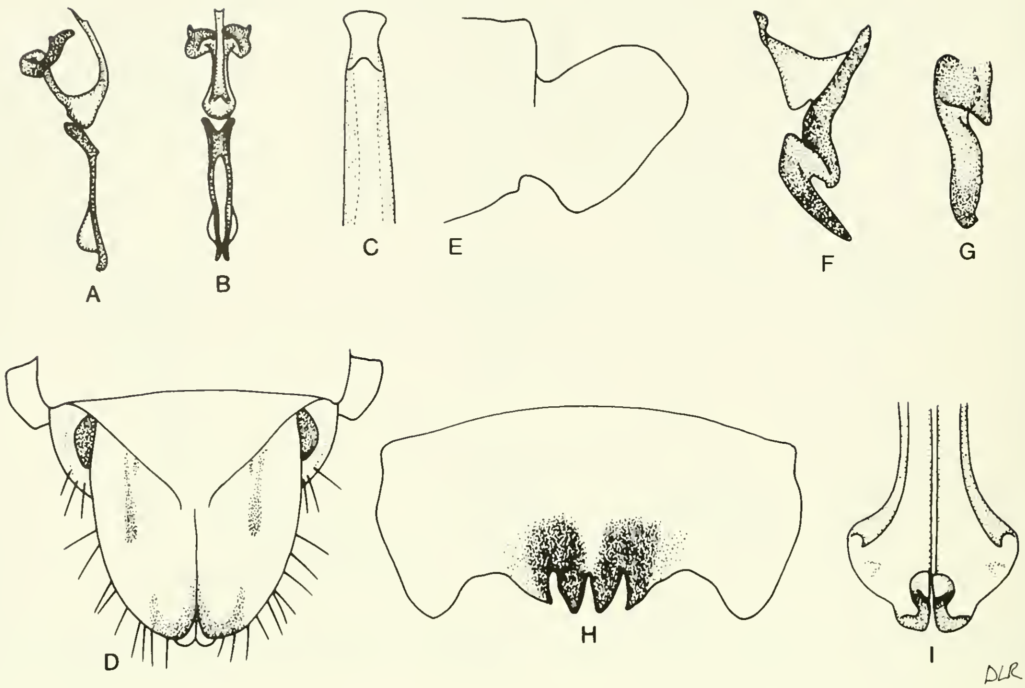


Fig. 16. *Flexamia gila*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

external genitalic characters and its geographic range. Other species (*doeringae, jacala*) of the *pectinata* group with somewhat similar male plates do not occur with *pectinata* in its range. Of the nine members of the group, only *mescalero* (host: *Muhlenbergia pauciflora*) and *collorum* (host: *Bouteloua uniflora*) have ranges that overlap the range of *pectinata*. The male plates (Fig. 11I) and female sternum VII (Fig. 14H) of *mescalero* distinguish it from *pectinata* (Figs. 11C, 14C). The male plates of *collorum* (Fig. 11G) differ from those of *pectinata* in general aspect and in the absence of the sclerotized ridge on the inner plate surface that characterizes *collorum*. The female sternum VII of *collorum* is similar to that of *pectinata*. Although the characters discussed above permit tentative recognition of the commonly encountered *pectinata*, definitive identification requires examination of the genitalia.

4. *Flexamia gila*, n. sp.

Length of ♂ 3.4 (3.1–3.7) mm, ♀ 3.8 (3.6–4.0) mm; head width of ♂ 1.03 mm, ♀ 1.08 mm. Crown not strongly produced; median length of crown approximately 0.63 x head width and 1.32 x interocular width (♂ n = 6; ♀ n = 4).

Crown light brown with dark, circular spot around apex, pale brown, transverse line on either side at middle. Pronotum light brown, usually with traces of four wide, longitudinal stripes. Elytra subhyaline, dark brown spot on disc; costal veinlets heavily margined with dark brown. Face black above, pale brown on lower portion.

MALE.—Pygofer (Fig. 16E) much as in *bandarita;* posterior margin slightly more produced. Plates (Fig. 16D) broad, gradually rounded from base to apex, extending to approximately 4/5 length of pygofer. Connective in lateral view with dorsal keels narrow (or rarely absent), approximately 1/4 height of dorsal apodeme; apodemal processes as in *bandarita;* styles (Fig. 16F) long, diverging apically in ventral aspect, preapical lobe rounded, produced ventrad and laterad; style

portion distad from preapical lobe gradually narrowing to embrowned, strongly divergent, acute apex in ventral aspect, or, in lateral aspect (Fig. 16G), appearing bladelike, produced ventrally and flattened, bearing minute teeth along the irregularly curved ventral margin of style ending in a truncate apex that is slightly curved ventrad. Aedeagus (Figs. 16B,C) symmetrical, short, slender. Apical margin flared and convex, much as in *pectinata*. Distance between gonopore and apex less than in *pectinata*. Gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 16H) with posterior margin broadly but shallowly emarginate, with four produced teeth; middle teeth broad. Ovipositor with basal processes of first valvulae (Fig. 16I) recurved; recurved portion constricted above proximal margin, expanded slightly mesad and distad into differentially sclerotized lobes.

TYPES.—Holotype ♂: New Mexico, Sierra Co., Kingston, 17 August 1985, R. F. Whitcomb (6,300 ft, IPL 001875, *Bouteloua curtipendula*). Paratypes: 3 ♂ and 1 ♀, same collection data; 2 ♂ and 2 ♀, Mexico, 5 km S Casas Grandes, Chihuahua (5,600 ft, *Bouteloua curtipendula*, 3 September 1987, A. L. Hicks, IPL 001774); 2 ♂ and 1 ♀, New Mexico, Socorro Co., Magdalena Mtns., Water Canyon, 7,000 ft., 16 August 1987, IPL 001756, A. L. Hicks. Deposited BARC, CNC, KSU, KU, OSU, and USNM.

REMARKS.—The aedeagal characters of *gila* are intermediate between those of *doeringae* and *pectinata*. The styles in *gila* are less produced ventrally than in *doeringae*. The longer, bladelike styles of *gila* differentiate males of *gila* from those of *pectinata;* females can be readily differentiated on the basis of the morphology of the female sternum VII and the bases of the first valvulae. The host of *gila* is *B. curtipendula*. The name *gila*, a noun in apposition, denotes the New Mexican mountains where the holotype was collected.

### 5. *Flexamia bandarita*, n. sp.

Length of ♂ 3.4 (3.3–3.5) mm, ♀ 3.7 (3.4–4.0) mm; head width of ♂ 1.09 mm, ♀ 1.04 mm; head not strongly produced; median length of crown 0.64 x head width and 1.33 x interocular width (n = 8 ♂, 3 ♀).

Color variable, ranging from very dark gray to pale, with irregular, dark markings on dorsum and forewings; face very dark with pale arcs on upper half; variable in lower half. Head stramineous in lighter specimens with paired, transverse lines at midpoint of crown and oblique markings at rear; venter and legs with irregular, fuscous markings.

MALE.—Pygofer strongly produced ventrally in rounded lobe; plates (Fig. 17D) contiguous on basal half, diverging apically into narrow V; extending to approximately 3/4 length of pygofer; style (Fig. 17F) heavily sclerotized, sinuate in ventral aspect, extending almost to the apex of the aedeagus, gradually narrowing to acute, ventrally directed, chelate apex (Fig. 17G) that is closely associated with sclerotized ridge on inner surface of each plate; connective in lateral aspect with dorsal keels narrow; aedeagus (Figs. 17B,C) symmetrical with slender shaft, straight in ventral aspect, without apical processes. Apex flared in caudoventral aspect, but varying from concave to convex. Dorsal apodemal process small, not attaining the plane of the shaft of the aedeagus, appearing suboval in caudodorsal aspect, with lobelike, converging, ventral apices. Gonopore minute, subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 17H) with inner teeth of the hind margin longer than outer pair. Ovipositor with basal processes of first valvulae (Fig. 17I) recurved.

TYPES.—Holotype ♂: Brewster County, Texas, Chisos Mountains, Big Bend National Park, Texas, 7 August 1987, R. F. Whitcomb (5,200 ft, *Bouteloua curtipendula*, IPL 003262). Deposited in USNM. Paratypes: 2 ♂, 1 ♀, same collection data; 1 ♂, Texas, Marathon Basin, 8 August 1984, deposited USNM, BARC, KSU, KU; 5 ♂, 1 ♀, Chisos Mountains, D. J. and J. N. Knull, 17 July 1946, deposited OSU.

REMARKS.—*Flexamia bandarita* resembles *pectinata*, *gila*, and *doeringae*, but the sinuate styles of *bandarita* separate it from these species. The middle teeth of the female sternum VII are longer than the outer pair, suggesting an intermediate stage in development of the median process that is present in *doeringae*. Like *pectinata* and *doeringae*, *bandarita* is a specialist of side-oats grama and, so far as known, is restricted to that host. Its known geographic range (Fig. 15) includes the higher, more mesic grasslands of the Chisos Mountains in Big Bend National Park and the

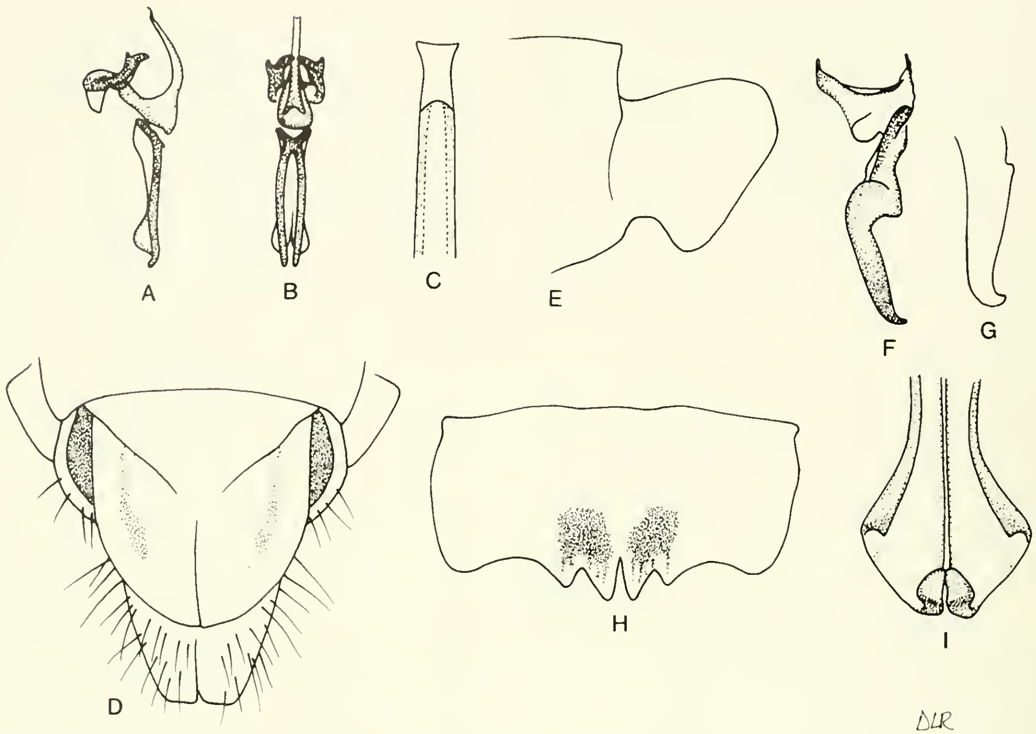


Fig. 17. *Flexamia bandarita*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

Marathon Basin north of the park. This region is rich in endemism presumably derived by insularization of high grasslands by desertification in the surrounding true Chihuahuan desert. All insects in our recent series, taken August 1987, are extremely dark; the season had been one of record rainfall, and vegetative growth of all plants in the Chisos Mountains was very lush.

The name *bandarita*, a noun in apposition, is one of the common names for side-oats grama in Mexico.

### 6. *Flexamia doeringae* Beamer & Tuthill

*Flexamia doeringae* Beamer & Tuthill 1934: 3.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (3.2–3.7) mm, of ♀ 3.7 (3.3–4.1) mm. Head produced (median crown length 1.40 x interocular width; 0.70 x head width) (♂ n = 20; ♀ n = 20). Face ivory with broad, black, basal, interocular line, occasional dark markings below. [♂] Plates (Fig. 11F) broad through most of their length, then narrowing sharply to rounded apices. Style with preapical lobe strongly developed, flattened and produced posteriorly; aedeagus (Fig. 12F) with protuberance near shaft apex close to tip in ventral aspect. [♀] Sternum VII (Fig. 14F) with inner teeth strongly produced and closely associated to form median process; ovipositor with each first valvula (Fig. 63A) recurved at base; recurved portion with transverse lobe cephalad of basal extremity.

GEOGRAPHIC DISTRIBUTION.—This species is known primarily from the mountains (Baboquivari, Catalina, Chiricahua, Huachuca, and Santa Rita ranges) of southeastern Arizona, but it also occurs in the Mexican highlands of Sonora and Chihuahua (Fig. 15). There is one record from Yavapai Co., Arizona (1 ♂, Granite Dell, 10 July 1933, R. H. Beamer).

BIOLOGY.—This species is apparently a

specialist on side-oats grama, *Bouteloua curtipendula*. Because this grass is a dominant in the mountains of southeastern Arizona and because many collectors have visited this region, *doeringae* is a common component of large *Flexamia* collections (Appendix I). The climate of the southeastern Arizona mountains is similar to that of the Mexican highlands but shows a definite Sonoran influence. *Flexamia doeringae* may therefore be a Sonoran vicariant that separated from the Chihuahuan *bandarita* and the prairie *pectinata*, which are also specialists of *B. curtipendula*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Bouteloua* 1.000; *Bouteloua curtipendula* 0.943 (n = 35).

REMARKS AND DIAGNOSIS.—The range of *doeringae* does not overlap that of any other member of the *pectinata* species group. This species can be readily distinguished by its ivory face, the pair of transverse lines on a pale, well-produced crown, and the structure of the external genitalia. The female sternum VII (Fig. 14F) is particularly distinct in having a medially produced structure consisting of a pair of long, central lobes and much shorter lobes on each side. The middle pair of teeth, in their size and degree of fusion, are maximally developed in this species.

### 7. *Flexamia collorum*, n. sp.

Length of ♂ 2.9 (2.7–3.0) mm, ♀ 3.0 (2.8–3.2) mm; head width of ♂ 0.87 mm, ♀ 0.89 mm. Crown not strongly produced; median length of crown 1.53 x head width and 0.68 x interocular width (♂ n = 11; ♀ n = 20).

Crown stramineous to light brown, pronotum with four faint, wide, brown stripes, forewings gray with irregular, dark markings. Face color and markings variable, without interocular line, but usually black in interocular area and lower area. Usually at least lorae pale. Crown with pair of oblique markings at rear, pair of transverse lines at midlength. Venter usually predominantly dark.

MALE.—Pygofer produced ventrally into an angulate lobe; caudoventral margin sloping dorsally to a broadly rounded, caudal lobe. Plates (Fig. 18D) short, extending to 1/2 length of pygofer, fused basally, contiguous medially for 2/3 length, acute apically. Plates produced on inner surface at about midlength into well-developed, sclerotized ridge that interfaces with style apices. Connective (Fig. 18A) in lateral view with dorsal keels narrow, approximately 1/3 height of dorsal apodeme; apodemal processes as in *bandarita;* style (Fig. 18F) short, abruptly narrowing beyond preapical lobe to avicephaliform, mesoventrally directed apices (Fig. 18G). Aedeagus (Figs. 18B,C) symmetrical, shaft slender, without processes, slightly flared apically in caudoventral aspect. Gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 18H) with four teeth on hind margin; outer pair not well developed, inner pair distinct, but short and rounded; ovipositor with basal processes of first valvulae (Fig. 18I) recurved.

TYPES.—Holotype ♂: Kimble Co., Texas, Junction, 14 September 1987, R. F. Whitcomb and R. C. Chambers (1,300 ft, IPL 003599, *Bouteloua uniflora*). Deposited USNM. Paratypes: 16 ♂, 19 ♀, same locality; Sutton Co., Texas, Roosevelt, 14 September 1987, 14 ♂, 31 ♀ (1,400 ft, IPL 003593, 003595, 003598). Deposited at KU, OSU, CNC, USNM, KSU, and BARC.

REMARKS.—*Flexamia collorum* is distinct from other members of the *pectinata* species group, from which it is readily separated by the short, avicephaliform style apices and by the extensively developed ridge on the inside of the male plates. It has been collected at several localities (Fig. 19) in the Texas hills (Edwards Plateau), where it appears to specialize on Nealley grama, *Bouteloua uniflora*. Nealley grama differs from side-oats grama in having single spikelets at the base of the rachis; it also has a narrow geographic distribution in Texas and Mexico. Although this species appears to intergrade with *curtipendula* in the Mexican state of Coahuila (Johnson 1943), it is readily distinguished from it in central Texas.

The name *collorum* is an adjective meaning "of the hills," in recognition of the Texas hills where it was discovered.

### 8. *Flexamia jacala*, n. sp.

Length of ♂ 3.5 mm; head width of ♂ 1.08 mm. Crown produced; length of crown 1.42 x interocular width, 0.75 x head width.

Color gray with irregular, dark markings on dorsum and forewings; face without black interocular band; crown with oblique, rear and transverse, midlength markings. Venter and legs dark with irregular, fuscous markings.

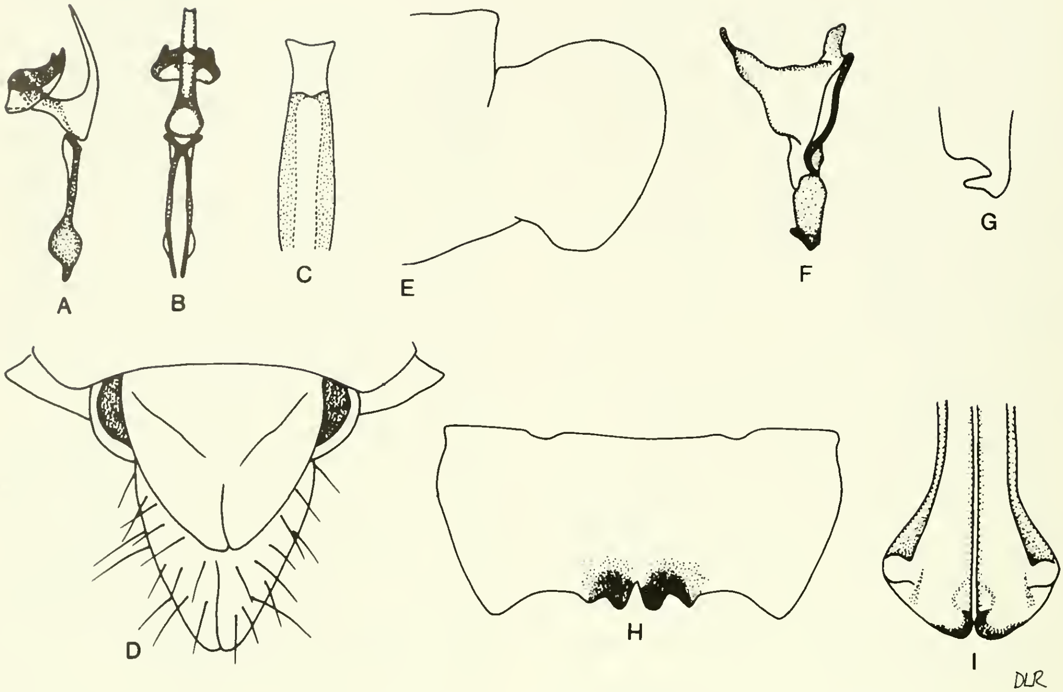


Fig. 18. *Flexamia collorum*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

MALE.—Pygofer (Fig. 20D) as in *bandarita*. Plates (Fig. 20G) extend to approximately 2/3 length of pygofer, fused basally, contiguous medially for 2/3 of their length, converging to bluntly rounded apices; male genitalia similar to those of *bandarita*, but styles (Fig. 20E) straight in ventral aspect instead of sinuate, diverging apically; apices abruptly turning ventrad, appearing avicephaliform in lateral aspect (Fig. 20F), preapical lobe of style produced laterally and caudally. Connective (Fig. 20A) in lateral view with dorsal keels narrow; apodemal processes as in *bandarita;* aedeagal tip (Fig. 20C) slightly flared in ventral view. Gonopore subapical on caudoventral surface.

TYPES.—Holotype ♂: Mexico, Jacala, Hidalgo, 13 August 1936, E. D. Ball. Deposited in USNM.

REMARKS.—This species is known from a single male. Nothing is known of its biology. It is most closely related to *bandarita*, from which it can be distinguished by its styles, which are straight in ventral aspect instead of sinuate; also, in lateral aspect the apices are avicephaliform instead of chelate. The name *jacala* is a noun in apposition denoting the type locality.

## 9. *Flexamia mescalero*, n. sp.

Length of ♂ 3.6 (3.5–3.9) mm, ♀ 3.8 (3.6–4.1) mm; head width of ♂ 1.07 mm, ♀ 1.12 mm. Crown moderately produced; median length of crown 1.42 x head width and 0.66 x interocular width (♂ n = 6; ♀ n = 16).

Color pale with brown markings. Crown ivory with pair of oblique markings on rear and pair of transverse lines at midlength; forewings pale gray with irregular, dark markings. Face variable, with or (more commonly) without black interocular band; specimens without band variably marked on face with brown or black.

MALE.—Pygofer (Fig. 21E) with posterior lobe angulate on ventral and caudal margins,

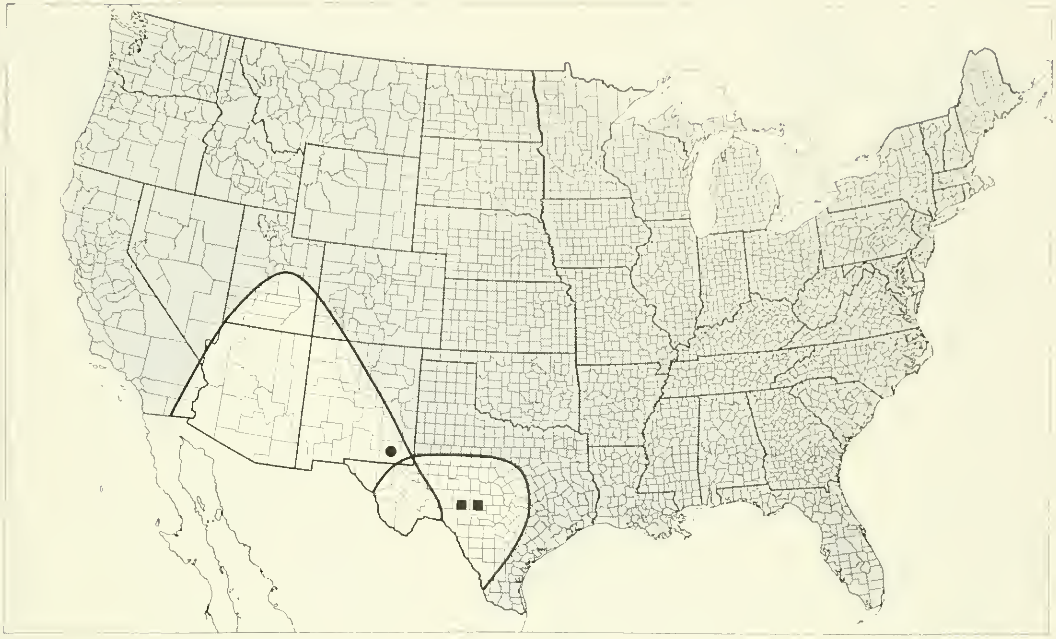

Fig. 19. Geographic distribution of *mescalero* (●) and *collorum* (■), with distribution of their hosts, *Muhlenbergia pauciflora* and *Bouteloua uniflora*, respectively.

slightly convex dorsally; plates (Fig. 21D) extending to approximately 4/5 length of pygofer, fused basally, diverging gradually along entire length; lateral margins tapering mesad to acute apices, inner surface with longitudinal groove and thickened mesal ridge along 3/4 of length, ending in small, embrowned tooth. Connective (Fig. 21A) in lateral view with dorsal keels narrow, approximately 1/4 height of dorsal apodeme; apodemal processes as in *bandarita;* styles (Fig. 21F) long in ventral aspect, slightly divergent distally, in lateral aspect with preapical lobe moderately produced and acute. Apical 1/2 of style flattened and minutely serrate basally, narrowing to ventromesally directed, calipterate apices (Fig. 21G), much as in *bandarita*. Aedeagus symmetrical, expanded apically in ventral aspect, appearing bluntly saggitate (Figs. 21C, 22), in lateral aspect slightly indented preapically; gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 21H) with posterior margin notched deeply, middle teeth very short and deeply inset, median incision deep, in some specimens divergent at margin. Ovipositor with bases of first valvulae (Fig. 21I) with sinuate, recurved processes that converge medially.

TYPES.—Holotype ♂: Eddy Co., New Mexico, 23 August 1985. A. L. Hicks and R. F. Whitcomb, 4,600 ft, IPL 001977, *Muhlenbergia pauciflora*. Deposited in USNM. Paratypes: 9 ♂, 16 ♀, same locality as holotype. Deposited at KU, KSU, OSU, CNC, BARC, and USNM.

REMARKS.—*Flexamia mescalero* is the only member of the *pectinata* group that has not been collected on *Bouteloua*. The unique aedeagal apex (Figs. 21C, 22) and female sternum VII (Fig. 21H) are diagnostic for this species, give it unique status in the group, and could justify treatment as a distinct group (see cladogram of Fig. 58). The host of this species is New Mexican muhly, *Muhlenbergia pauciflora*. Attempts to find other localities for this species have been unsuccessful.

The name *mescalero* is a noun in apposition honoring the Native American Mescalero Apache nation, which inhabited the mountains of southeastern New Mexico in the pre-Columbian era and which is today

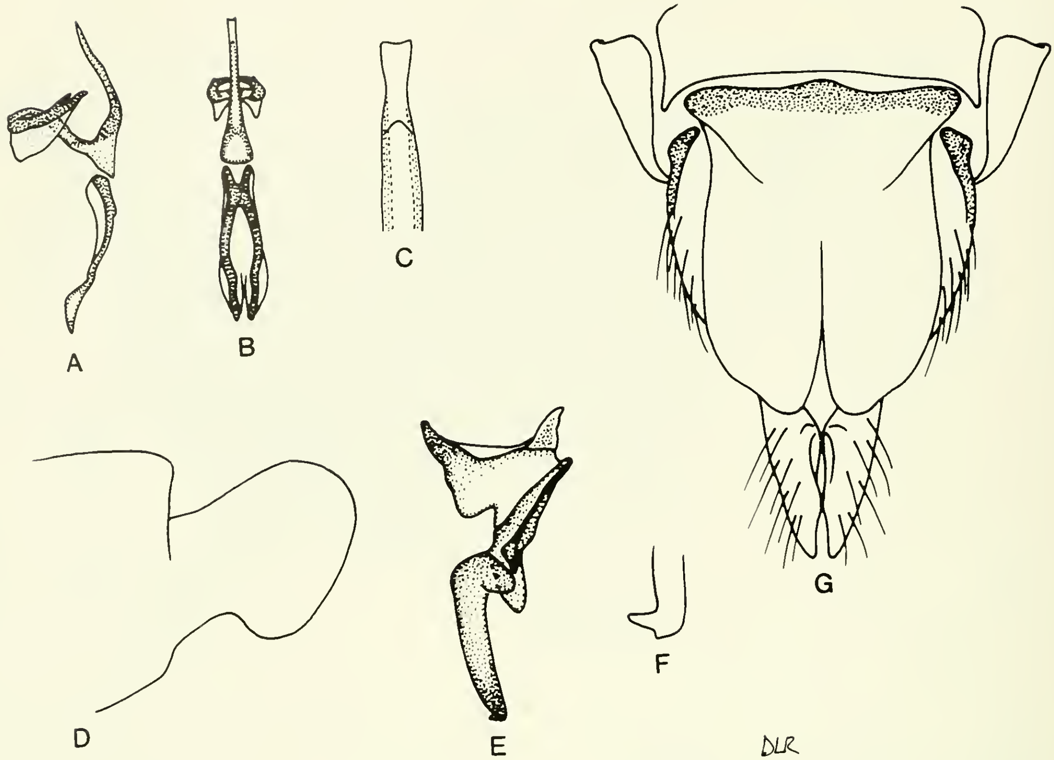


Fig. 20. *Flexamia jacala*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, apex of right style, lateral aspect; G, male plates and pygofers, ventral aspect.

establishing high standards for judicious management of tribal lands.

## II. The *abbreviata* Group

The *abbreviata* group consists of a single, widespread species that specializes on *Bouteloua* spp. The morphology of the aedeagal apex constitutes an autapomorphy that defines the monobasic group.

### 10. *Flexamia abbreviata* (Osborn & Ball)

*Deltocephalus abbreviatus* Osborn & Ball 1897: 206.
*Deltocephalus (Flexamia) abbreviatus*, DeLong 1926: 33.
*Flexamius abbreviatus*, DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.8–3.4) mm, of ♀ 3.2 (2.9–3.6) mm. Head moderately produced (mean crown length 1.26 x interocular width, 0.61 x head width) (♂ n = 20; ♀ n = 20). Face without distinct interocular line (but very rarely with a brown band contrasting with a pale face). Face often with parallel, sinuate, brown lines. [♂] pygofer (Fig. 62H) strongly constricted, posterior lobe strongly produced on upper portion of posterior margin. Plates (Fig. 8E) shield-shaped, about 0.65 x pygofer length. Aedeagus (Fig. 7H) with elongate, anteapical gonopore on caudoventral surface, apex with pair of short, truncate processes curved cephalad, apodemal processes each with broad, membranous, apical expansion. [♀] Sternum VII (Fig. 10E) with a medial, truncate projection, which has a median incision that is almost always decorated on either side by a pair of infuscated spots.

GEOGRAPHIC DISTRIBUTION.—This species occurs (Fig. 23) from the Canadian prairie provinces to Montana, Utah, southwestern Nevada, Wisconsin, Illinois, Oklahoma, Texas, and Durango, Mexico (1 ♂, 27 mi N LaZarca, 27 October 1981, M. W. Nielson).

BIOLOGY.—Because of the dominance of its *Bouteloua* hosts, the densities it achieves on these hosts, and the accessibility of its hosts to

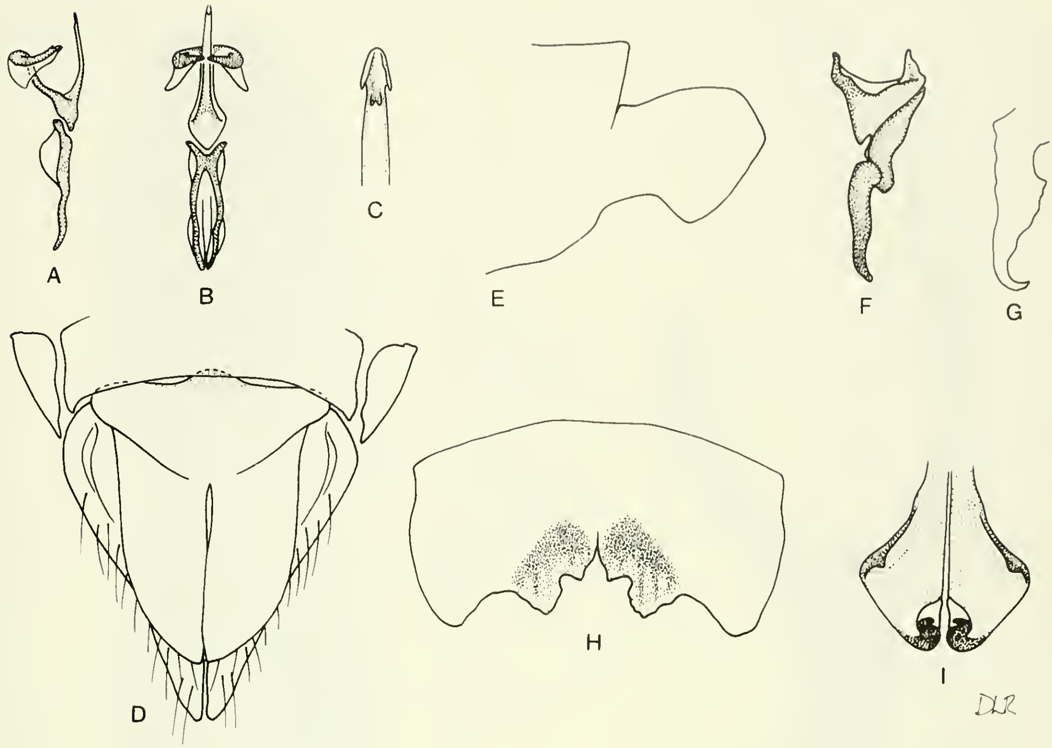


Fig. 21. *Flexamia mescalero*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, caudoventral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

collectors, this is the most frequently collected *Flexamia* species (Appendix I). In the northern and western parts of its range it is a specialist on blue grama (*Bouteloua gracilis*), and the range of this grass limits its distribution (Fig. 23). In Chihuahuan grasslands and montane islands of southern Arizona and New Mexico, it is an inhabitant of mixed *Bouteloua* grasslands, where it may occur on blue, hairy (*B. hirsuta*), or, more rarely, black (*B. eriopoda*) grama. In the eastern prairie where the grasslands form a mosaic with patches of eastern deciduous forest, the only known host is hairy grama; the eastern boundary of the range of *abbreviata* is determined by this host. In the Edwards Plateau of Texas, *abbreviata* occurs on *B. hirsuta*, *B. pectinata*, *Muhlenbergia reverchonii* (seep muhly), and perhaps other chloridoid grasses.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.936; *Bouteloua* 0.836. Prairie: *Bouteloua* 0.780; *B. gracilis* 0.745 (n = 428); mixed *Bouteloua* grasslands: *B. gracilis* 0.317, *B. hirsuta* 0.568 (n = 347).

REMARKS AND DIAGNOSIS.—Males and females of this species can be recognized by the combination of their small size, brown face without interocular band, and unique morphologies of the sternum VII or male plates and pygofer (Fig. 8E). The hind margin of the female sternum VII (Fig. 10E) contains four teeth, a condition we believe to be homologous with similar structures in the *pectinata* group. *Flexamia abbreviata* occurs with *curvata* (host: *Buchloë dactyloides*) throughout much of the range of *Buchloë*. Dark male specimens of *curvata* are occasionally confused with *abbreviata* but can be tentatively recognized without dissection by characters of the plates and pygofers.

### III. The *zacate* Group

The *zacate* group consists of two species that specialize on bush muhly (*Muhlenbergia*

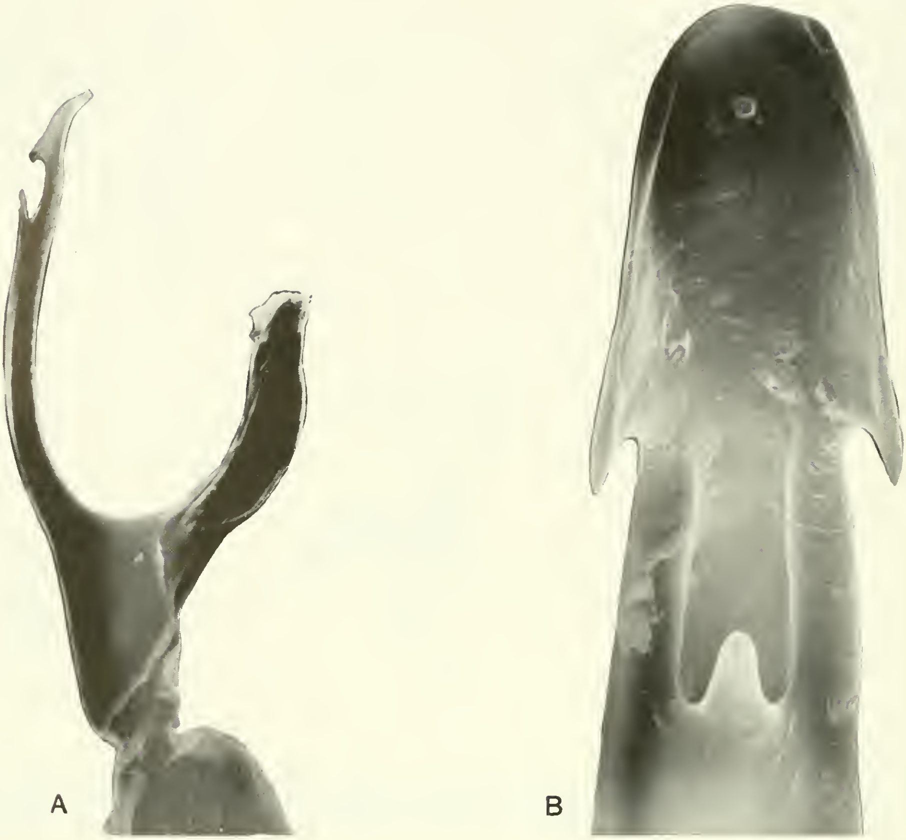


Fig. 22. Scanning electron micrograph of aedeagus of *Flexamia mescalero:* A, lateral aspect (312X); B, ventral aspect of aedeagal apex (1680X).

*porteri*). These sister species are distinguished on the basis of their posteriorly produced male pygofers, curved aedeagus lacking apical processes, and elongate, but rounded male plates. No other *Flexamia* species has this combination of characters.

### Description of the *zacate* Group

Medium-sized. Length of ♂ 3.2–4.1 mm, of ♀ 3.6–4.1 mm. Dorsum brown. Crown moderately produced. [♂] Plates elongate, but only about 2/3 length of pygofer, fused basally, narrowing continuously to apices. Pygofer (Figs. 25E, 62I) with posterior lobe strongly produced posteriorly. Aedeagus and connective (Fig. 6C) distinctly articulated. Aedeagus curved in lateral aspect, without apical processes (Fig. 25A). [♀] Sternum VII (Figs. 10I, L) with deep, median incision.

### Key to Species of *zacate* Group

1. Males .................................... 2
— Females .................................... 3
2(1). Aedeagus (Fig. 7I) narrow in ventral and lateral aspects; gonopore (Fig. 24) long and narrow, extending along apical third of shaft .................. *zacate*, n. sp.
— Aedeagus (Figs. 6C, 7J) wide, scimitar-shaped in lateral aspect, diamond-shaped in ventral aspect. Gonopore not elongate, near midpoint of shaft ............ *canyonensis* Young & Beirne
3(1). Hind margin of sternum VII (Fig. 10L) with outer pair of teeth essentially absent, fused with medial teeth to form median projection ...... *zacate*, n. sp.
— Hind margin of sternum VII (Fig. 10I) with outer teeth distinct, rounded ............... *canyonensis* Young & Beirne

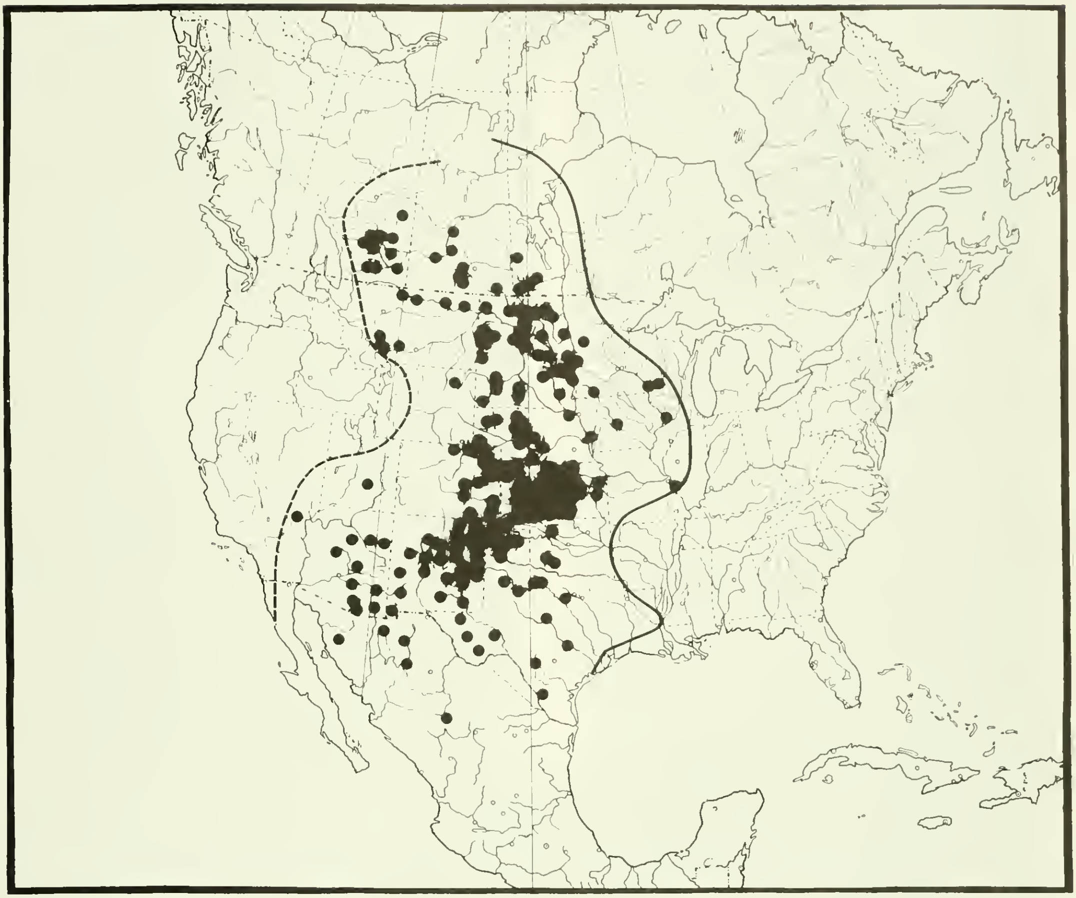

Fig. 23. Geographic distribution of *abbreviata*. Western limit is defined by the range of *Bouteloua gracilis*. Eastern limit is defined by the range of *Bouteloua hirsuta*. Host relationships in Mexico are unknown.

11. *Flexamia canyonensis* Young & Beirne

*Flexamia canyonensis* Young & Beirne 1958: 18.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.5–4.1) mm, of ♀ 3.9 (3.8–4.1) mm. Head moderately produced (1.29 x interocular width; 0.68 x head width) (♂ n = 4; ♀ n = 5). Face with clypeus and dorsal portion of genae black. Clypeus, lora, and lower part of genae pale yellow. [♂] Pygofer (Fig. 62I) as in *abbreviata*. Plates (Fig. 9C) gradually narrowing apically to rounded apices. Aedeagus symmetrical, scimitar-shaped in lateral aspect, diamond-shaped in ventral aspect. Gonopore on ventral surface of aedeagus, near midpoint of shaft. [♀] Sternum VII with deep, median incision on hind margin. Ovipositor with bases of each first valvula (Fig. 63H) strongly recurved, processes sinuate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—*Flexamia canyonensis* has been collected at Sabino Canyon, Arizona (E. D. Ball), and in our own studies at Kingman, Portal, and Santa Rita Experimental Range, Arizona (Fig. 26).

BIOLOGY.—Our collections of *canyonensis* are from bush muhly, *Muhlenbergia porteri*. This grass is common in the type locality, and we assume that it is the sole host. *Flexamia canyonensis* appears to be restricted to the highlands of the Sonoran Desert. This species and its Chihuahuan sister, *zacate*, are among the few *Flexamia* species to colonize semiarid habitats. Perhaps *canyonensis* is protected from desiccation by the microclimate

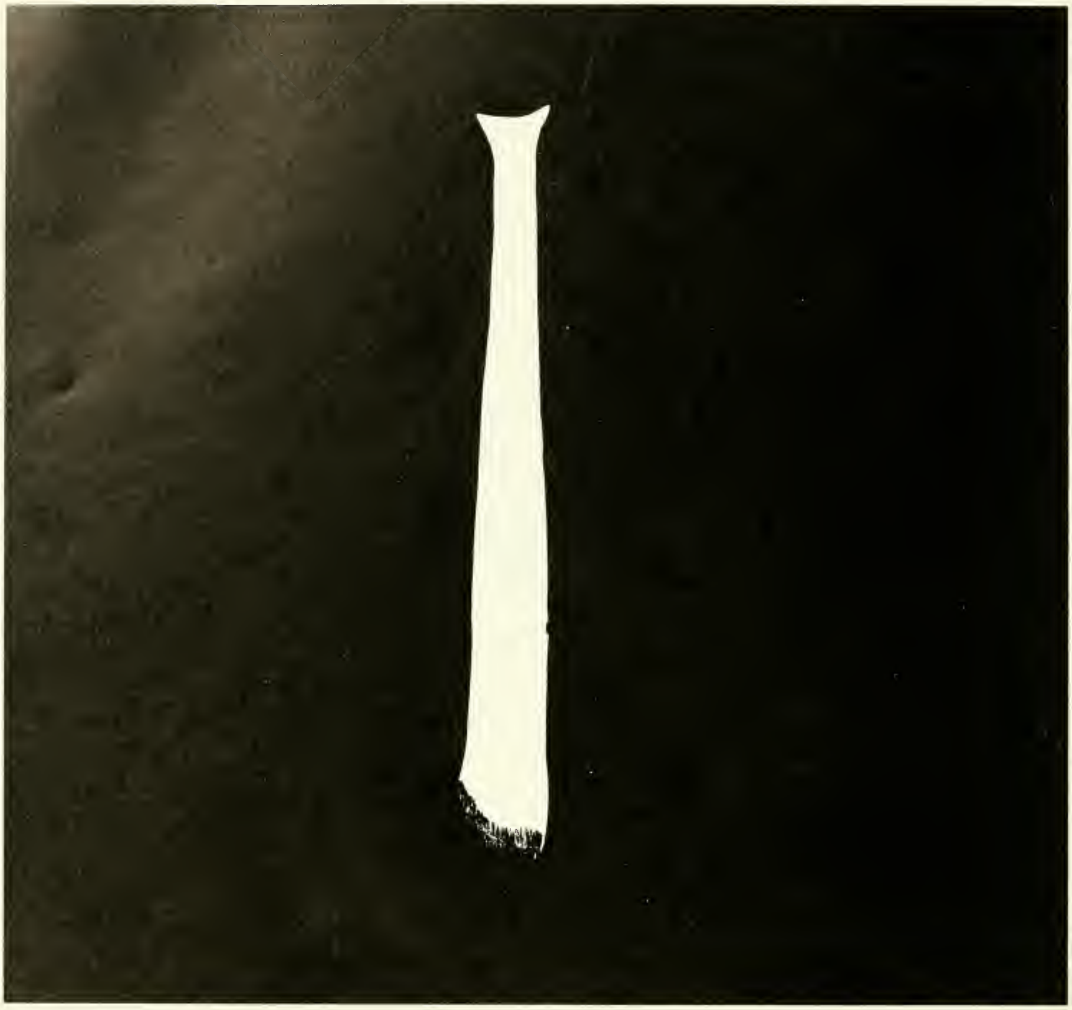

Fig. 24. Scanning electron micrograph of aedeagal apex of *Flexamia zacate*, ventral aspect (800X).

produced by its host, which grows within protective shrubs.

OLIGOPHAGY COEFFICIENTS.—*Muhlenbergia porteri* 1.00 (n = 9, 3 series).

REMARKS AND DIAGNOSIS.—Females can be easily recognized by their distinctive sternum VII (Fig. 10I), which bears a deep, median incision. Males can be tentatively recognized by their characteristic face pattern and produced, flattened pygofer. The aedeagus of *canyonensis* is unique.

### 12. *Flexamia zacate*, n. sp.

Length of ♂ 3.5 (3.2–3.9) mm, ♀ 3.8 (3.6–4.0) mm; head width of ♂ 1.04 mm, ♀ 1.08 mm. Crown produced; median length of crown 1.48 x head width and 0.71 x interocular width (♂ n = 37; ♀ n = 12).

Dorsum ivory. Crown with at least trace of oblique, basal and midlength, transverse lines. Face without black interocular line, black in interocular area with at most pale arcs, bottom of face brown, with irregular, pale markings. Venter stramineous with irregular markings.

MALE.—Pygofer (Fig. 25E) with weakly developed constriction before posterior lobe, ventral lobe small, caudoventral margin produced posteriorly, dorsal margin unevenly convex. Plates (Fig. 25D) extending to approximately 2/3 length of pygofer, fused basally, contiguous medially for 1/2 length, acute apically; connective in lateral view (Fig. 25A) with dorsal keels narrow, approximately

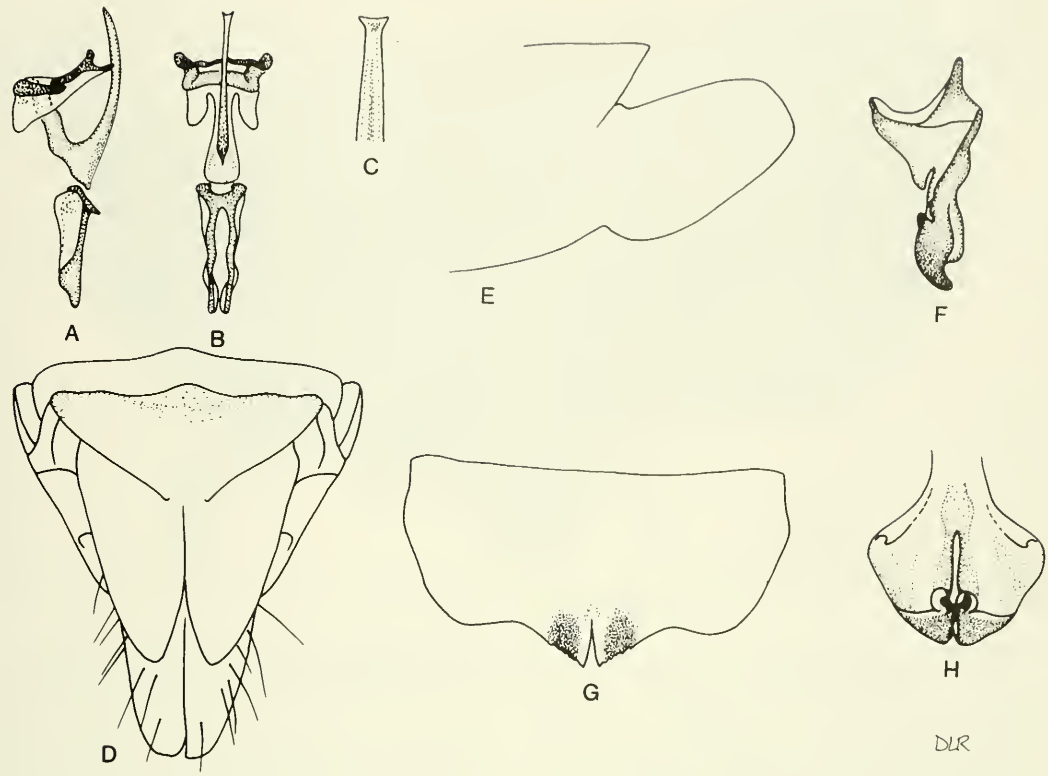


Fig. 25. *Flexamia zacate*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, female sternum VII; H, bases of first valvulae of female, dorsal aspect.

1/4 height of dorsal apodeme, with distinctive, minute tooth on ventral surface, anterior to distinct joint with the aedeagus; apodemal appendages campanulate in caudal aspect, with very slender, anteapical processes directed mesad; styles (Fig. 25F) with apex digitate, curving sharply ventrad, each bearing small preapical tooth on mesal surface; preapical lobe not produced. Aedeagus symmetrical, shaft slender and cylindrical without processes, curving gradually caudodorsad in lateral aspect, appearing straight in ventral aspect. Apex slightly flared in caudoventral aspect, flattened in lateral aspect, with apical margin concave. Gonopore (Figs. 24, 25C) long and narrow, extending along apical third of caudoventral surface of shaft.

FEMALE.—Sternum VII (Fig. 25G) with posterior margin produced medially, with deep, median incision; ovipositor with basal processes of first valvulae (Fig. 25H) with broad portions close to base.

TYPES.—Holotype ♂: Brewster County, Texas, Big Bend National Park (Panther Junction), 26 August 1985 (3,600 ft, R. F. Whitcomb and A. L. Hicks; IPL 002093). Deposited USNM. Paratypes: 33 ♂, 10 ♀, same locality and date, IPL 002057, 25 August 1985; 13 ♂, 4 ♀, same locality and date, deposited USNM, BARC, CNC, KU, KSU, and OSU. Thirty-five immature specimens (IPL 002057) have also been deposited with the paratypes.

REMARKS.—This species is a sister to *canyonensis* but can be distinguished from it by the shape of the aedeagus, which, though curved, is much narrower in lateral aspect and is not diamond-shaped in ventral aspect. The length of the gonopore of *zacate* also separates it from *canyonensis*. Both *canyonensis* and

Fig. 26. Geographic distribution of *canyonensis* (●) and *zacate* (■) and their host, *Muhlenbergia porteri*.

*zacate* are apparently specialists on bush muhly, *Muhlenbergia porteri*. This grass occurs chiefly in association with thorny shrubs such as *Acacia*, *Prosopis*, *Larrea*, or *Opuntia*, which defend it against large herbivores. The entire volume of the host shrub may be filled with the tangled culms of bush muhly; eventually the host shrub dies, presumably from competition. Because of its unique habitat, *zacate* is difficult to collect without a vacuum-collecting device. The name *zacate* is a noun in apposition denoting various grasses of the *Muhlenbergia* or *Sporobolus* types. Bush muhly is known in Mexico as "zacate arana" (spider grass).

## IV. The *grammica* Group

The *grammica* group consists of a single, distinctive species. The morphology of the aedeagal apex and the female sternum VII provides autapomorphies that define the group.

### 13. *Flexamia grammica* (Ball)

*Deltocephalus grammicus* Ball 1900: 204.
*Deltocephalus (Flexamia) grammicus)*, DeLong 1926: 37.
*Flexamius grammicus*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 4.5 (4.1–5.0) mm, of ♀ 4.6 (4.3–5.0) mm. Head not strongly produced (mean crown length 1.08 x interocular width, 0.54 x head width) (♂ n = 20; ♀ n = 20). Dorsum (Fig. 2C) with three pairs of longitudinal, dark stripes, median pair extending from hind portion of the crown posteriorly through the scutellum and wings. Face stramineous with single, black interocular line. [♂] Pygofer (Fig. 62O) with narrow, posterior lobe, dorsal more prominent than ventral constriction in lateral aspect. Plates (Fig. 8F) broad, contiguous, parallel-sided for much of their length, broadly rounded apically. Aedeagus asymmetrical with anteapical gonopore on anterodorsal surface, with pair of recurved processes (Fig. 7E), one edentate on the side of shaft near gonopore, one at the shaft apex. [♀] Sternum VII (Fig. 10F) broadly and shallowly concave on posterior margin.

GEOGRAPHIC DISTRIBUTION.—*Flexamia grammica* occurs in southern Alberta and Saskatchewan south through the Great Plains to Texas (Fig. 27).

BIOLOGY.—In the northern part of its range, *grammica* is a specialist on prairie sandreed, *Calamovilfa longifolia*. In the southern part of its range, it specializes on *C. gigantea*.

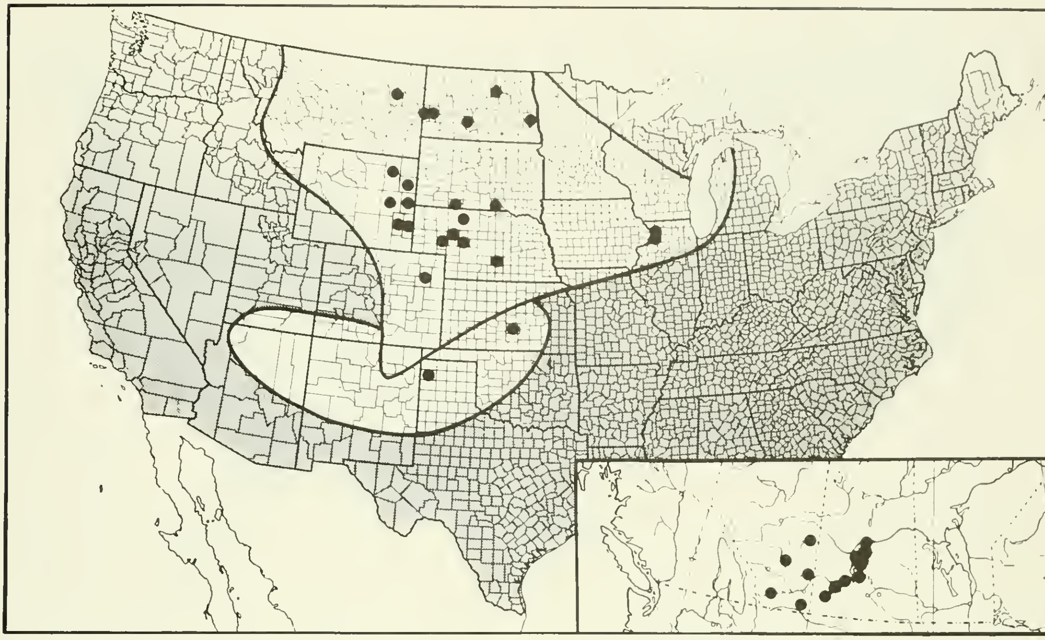

Fig. 27. Geographic distribution of *Flexamia grammica*, and two hosts, *Calamovilfa longifolia* (northern prairie) and *C. gigantea* (southern prairie and Southwest).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Calamovilfa* spp. 0.872 (n = 47).

REMARKS AND DIAGNOSIS.—The habitus of *grammica* is distinctive, as is its size.

## V. The *curvata* Group

The *curvata* group consists of two closely related sister species that specialize on buffalograss, *Buchloë dactyloides*. One (*curvata*) is adapted to temperate regions, whereas the other (*surcula*) is adapted to the subtropical climate of south Texas and Mexico. In the following description synapomorphies are designated [s].

### Description of the *curvata* Group

Small, deltocephaline leafhoppers. Length of ♂ 2.4–3.5 mm, of ♀ 2.6–3.9 mm. Usually stramineous in color, but occasionally much darker. [♂] Pygofer (Figs. 62K,L) somewhat produced caudodorsally. Plates (Figs. 9D,E) short, shield-shaped, about half length of pygofer. Aedeagus (Figs. 7F,G) [s] with two pairs of apical processes; style apex [s] foot-shaped in broadest aspect. [♀] Female sternum VII (Figs. 10J,K) with median incision or notches, with infuscation surrounding or bordering notch or incision.

### Key to Species of *curvata* Group

1. Males . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
— Females . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2(1). Gonopore small, subcircular, opening near aedeagal apex; apical pair of processes short (Fig. 7G) . . . . . . . . . . *surcula* DeLong & Sleesman
— Gonopore elongate; apical pair of processes much longer (Fig. 7F) . . . . . . . . . *curvata* DeLong
3(1). Female sternum VII (Fig. 10K) with completely infuscated, median incision . . . . *curvata* DeLong
— Female sternum VII (Fig. 10J) notched, but without median incision; infuscated on each side of notches . . . . . . . . . *surcula* DeLong & Sleesman

## 14. *Flexamia surcula* DeLong & Sleesman

*Flexamius* [sic] *surculus* DeLong & Sleesman 1929: 99.

IMPORTANT CHARACTERS.—Length of ♂ 3.0 (2.6–3.4) mm, of ♀ 3.4 (2.9–3.7) mm. Head moderately produced (mean crown length 1.35 x interocular width; 0.68 x head width) (♂ n = 20; ♀ n = 20). Face stramineous, except for broad, brown, basal, interocular

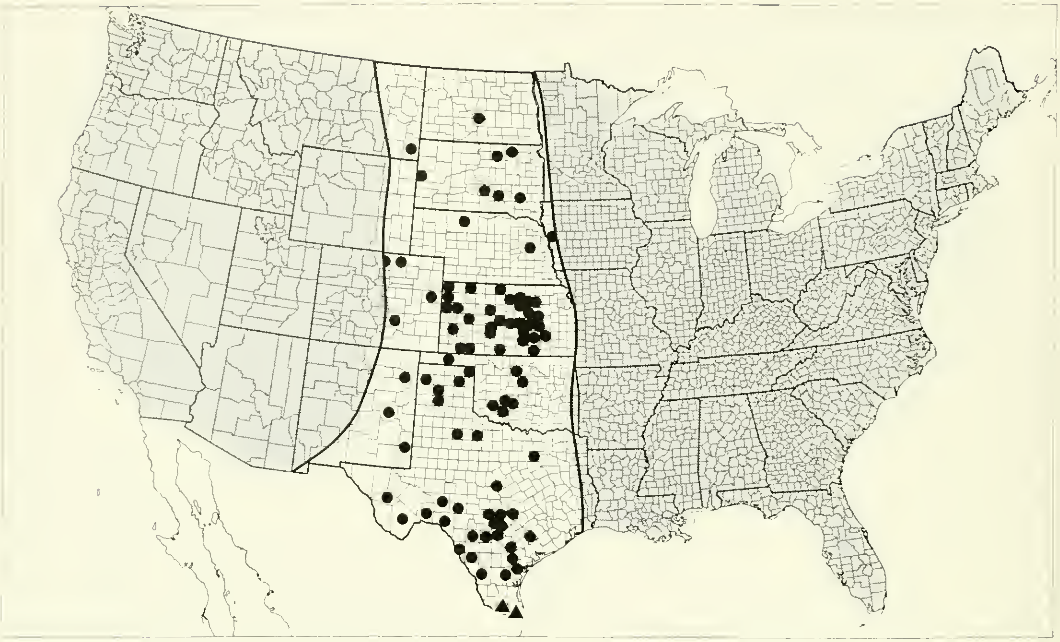

Fig. 28. Geographic distribution of *Flexamia curvata* (●) and *surcula* (▲) and their host, *Buchloë dactyloides*.

line. [♂] Pygofer (Fig. 62L) with posterior lobe strongly produced; style with apical portion foot-shaped, but longer than in *curvata*. Plates (Fig. 9E) as in *curvata*. Aedeagus (Fig. 7G) with pair of recurved, apical processes, shorter than in *curvata*, and pair of anteapical processes. [♀] Sternum VII (Fig. 10J) infuscated on either side of shallow notch. Ovipositor with each first valvula (Fig. 63I) with basal portion curved dorsad through more than 90 degrees, recurved portion oblique and crescentiform in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Subtropical Texas, and probably coastal prairies of northeastern Mexico (Fig. 28).

BIOLOGY.—*Flexamia surcula* is restricted to subtropical grasslands. We have collected it from *Buchloë* in the Rio Grande Valley in Cameron and Hidalgo counties of south Texas. Collection records from December, January, and February indicate that this species does not diapause and probably breeds more or less continuously throughout the season as host condition permits.

REMARKS AND DIAGNOSIS.—This species is closely related to *curvata*. We have referred a specimen labeled "paratype" from San Antonio, Texas, in the OSU collection to *curvata*. The sternum VII of *surcula* females lacks the deep, median incision of *curvata*.

### 15. *Flexamia curvata* DeLong

*Deltocephalus (Flexamia) curvatus* DeLong 1926: 34.
*Flexamius curvatus*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.4–3.5) mm, of ♀ 3.4 (2.6–3.9) mm. Head moderately produced (mean crown length 1.33 x interocular width; 0.63 x head width) (♂ n = 21; ♀ n = 23). Face usually pale brown, often with traces of indistinct, brown interocular band. [♂] Pygofer (Fig. 62K) with posterior lobe simple, somewhat produced caudodorsally. Plates (Fig. 9D) short, shield-shaped. Style foot-shaped in broadest aspect. Aedeagus (Fig. 7F) subsymmetrical, recurved anterior processes extending basad almost to midlength of shaft, pair of shorter apical processes not in bilaterally symmetrical plane; gonopore an elongate channel on caudoventral surface. Recurved anteapical processes extending basad almost to middle of shaft; pair of shorter apical processes extending basad. [♀] Sternum VII (Fig. 10K) with hind margin concave on each side of median incision. Ovipositor with base of each first valvula

(Fig. 63F) bearing posteriorly directed, slender process.

GEOGRAPHIC DISTRIBUTION.—*Flexamia curvata* occurs throughout much of the temperate range of its host, *Buchloë dactyloides* (Fig. 28).

BIOLOGY.—This species often occurs in large populations on *Buchloë*, where it is a member of a guild that also includes *Athysanella*, *Polyamia*, *Laevicephalus*, and *Gillettiella* species (Whitcomb et al. 1987). In the subtropical part of the range of buffalograss (in south Texas and, presumably, Mexico), *curvata* is replaced by *surcula*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.986; *Buchloë dactyloides* 0.925 (n = 560).

REMARKS AND DIAGNOSIS.—This species is readily recognized by the combination of its small size and external genitalic characteristics. Most specimens are light stramineous, with conspicuous, black spots in the middle and apical cells of the forewing (Fig. 4B); these specimens are unmistakable. Very large male specimens of *curvata* might be confused with *inflata*, whose plates and pygofer are superficially similar. However, *inflata*, which like *curvata* is usually light stramineous in color, never has a dark spot in the center of the forewing. Dark specimens of *curvata* are occasionally referred erroneously to *abbreviata*.

## VI. The *picta* Group

This group consists of two species, each with a distinctive habitus, which can be unambiguously designated as sister species on the basis of the morphology of the male aedeagus and pygofer, and the indistinct articulation between the aedeagus and connective. In addition, both species feed on *Aristida*. One (*pyrops*) has, perhaps, the most distinctive habitus in the genus (Fig. 2E), but *picta* can also be recognized without dissection. In the following description synapomorphies defining the group are designated [s].

### Description of the *picta* Group

Medium-sized or large, deltocephaline leafhoppers. Length of ♂ 2.9–4.0 mm, of ♀ 2.9–4.9 mm. Crown variably produced (in *pyrops*, reaching more than 2 x interocular width). [♂] Pygofer [s] notched on dorsal margin, posterior lobe angulate, sharply produced. Plates small in relation to large pygofers; [s] joint between aedeagus and connective indistinct. Aedeagus symmetrical, shaft elongate, [s] apex capitate, pair of slender, recurved, anteapical processes with entire edges. Gonopore subapical on caudoventral surface.

### Key to Species of *picta* Group

1. Head produced, with crown more than twice interocular width (Fig. 2E) . . . . . . *pyrops* (Crumb)
— Head only moderately produced . . *picta* (Osborn)

## 16. *Flexamia picta* (Osborn)

*Deltocephalus pictus* Osborn 1907: 165.
*Deltocephalus funabulus* Crumb 1915: 189.
*Deltocephalus (Flexamia) pictus*, DeLong 1926: 32.
*Flexamius* [sic] *pictus*, DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (2.9–4.0) mm, of ♀ 3.6 (2.9–4.2) mm. Head moderately produced (1.38 x interocular width; 0.64 x head width) (♂ n = 24; ♀ n = 20). Face pale yellow, with broad interocular band. Forewings usually dark gray, contrasting with lighter crown and pronotum, dark-pigmented spot in apex. [♂] Pygofer (Fig. 5A) similar to that of *pyrops*. Plates (Fig. 9A) very short, only about 1/3 length of pygofer, narrowed apically. Aedeagus and connective with indistinct joint with the connective, gonopore subapical on caudoventral surface. Aedeagal apex capitate; expanded portion with a few small teeth; pair of slender, recurved, anteapical processes with entire edges arising on each side of gonopore. [♀] Sternum VII with median projection. Ovipositor with base of each first valvula (Fig. 63J) curved through 180 degrees, obliquely bisinuate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—This species occurs throughout much of the Southeast, from Massachusetts to Kansas, and south through the mixed prairie to Texas (Fig. 29).

BIOLOGY.—*Flexamia picta* appears to be associated with *Aristida* spp. Some of the colonized species are annuals. This is a unique situation in *Flexamia* hosts; all other known hosts are perennials.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.919; *Aristida* spp. 0.870 (n = 285).

REMARKS AND DIAGNOSIS.—It is important for students of the genus to learn the habitus of *picta*, which is very common throughout much of its range. This species can be recognized by the combination of a dark-pigmented

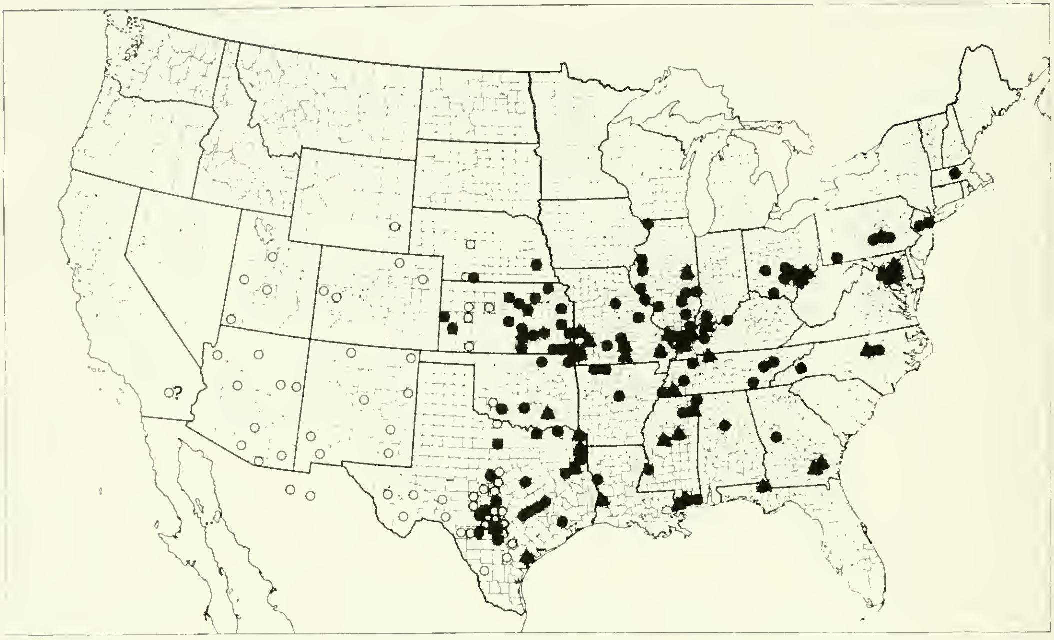


Fig. 29. Geographic distribution of three *Aristida* specialists: *Flexamia arizonensis* (○), *pyrops* (▲), and *picta* (●).

spot in the apex of the forewing (Fig. 4C) in combination with the face characteristics. The face is usually sordid yellow but occasionally is light gray or very pale brown. A few dark individuals of certain other species (e.g., *clayi*) may have a similar wing spot, but if so, the face is never pale. The geographical distribution of *picta* (southeastern) is also usually indicative. The range of *picta* overlaps the ranges of *flexulosa* and *arizonensis*, which have superficially similar faces, only in central Texas, Oklahoma, and Kansas. Finally, the small male plates, which contrast with very large pygofers, are diagnostic for *picta*. Thus, dissection is usually unnecessary for recognition of this species.

### 17. *Flexamia pyrops* (Crumb)

*Deltocephalus pyrops* Crumb 1915: 191.
*Deltocephalus (Acurhinus) pyrops*, DeLong 1926: 21.
*Acurhinus pyrops*, DeLong 1948: 226.
*Flexamia pyrops*, Oman 1949: 167.

IMPORTANT CHARACTERS.—Length of ♂ 3.8 (3.6–4.0) mm, of ♀ 4.2 (3.8–4.9) mm. Head very strongly produced (crown length 2.19 x interocular width, 1.00 x head width) (♂ n = 20; ♀ n = 20). Face stramineous, interocular line with three or more short, dentate projections from lower margin. [♂] Pygofer (Fig. 5B) with distinct notch on dorsal margin, posterior lobe produced ventrad in conspicuous, acute process; plates (Fig. 9B) very short, no more than 1/3 length of pygofer, rounded apically. Joint between connective and aedeagus not well developed. Aedeagus symmetrical, gonopore on caudoventral surface, pair of recurved, anteapical processes arising basad of gonopore. Apex of shaft (Fig. 7L) capitate, similar to that of *picta*, but with fewer, more distinct teeth. [♀] Sternum VII (Fig. 10H) with hind margin conspicuously concave at middle.

GEOGRAPHIC DISTRIBUTION.—Although this is a southeastern species, it occurs as far north as Pennsylvania, Ohio, Illinois, and Kansas (Fig. 29).

BIOLOGY.—*Flexamia pyrops*, like *F. picta*, is closely associated with *Aristida* spp., but the two species are seldom found together. The type of *pyrops* from Tennessee was taken on "*Aristida longespica*." In Illinois the host was *A. dichotoma* var. *curtisii* (Whitcomb 1957).

REMARKS AND DIAGNOSIS.—The habitus of *pyrops* is unique and diagnostic.

## VII. The *albida* Group

The *albida* group comprises two species that are very distinct in general facies and geographic distribution. Common characteristics of the species are their patterns of dorsal stripes, face patterns, and their bifurcate, apical, aedeagal processes (an apomorphy shared with *serrata*). The morphology of the male pygofers of the species may constitute a synapomorphy. The biology of *albida* and *slossonae* appears to be more complex than that of many other *Flexamia* species. The dorsal stripes, face patterns, and large size of these species suggest that they may have arisen from an ancestor related to *Spartopyge*.

### Description of the *albida* Group

Medium-sized to large. Length of ♂ 3.4–4.2 mm, of ♀ 3.6–4.8 mm. Dorsum with distinctive pattern of stripes extending from head across pronotum, scutellum, and forewings. Face pale with black interocular band. Male pygofer with poorly differentiated posterior lobe. Aedeagus with pair of bifurcate, apical appendages, unpaired ventral process.

#### Key to Species of the *albida* Group

1. Forewings rounded, male plates (Fig. 8A) not exceeding pygofer, female sternum VII not trilobed; prairie ......... *albida* (Osborn & Ball)

— Forewings obliquely truncate, male plates exceeding pygofer (Fig. 8B); female sternum VII trilobed (Fig. 10B); Florida ...... *slossonae* (Ball)

### 18. *Flexamia albida* (Osborn & Ball)

*Deltocephalus albidus* Osborn & Ball 1897: 201.
*Deltocephalus (Flexamia) albidus*, DeLong 1926: 36.
*Flexamius albidus*, DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.4–3.9) mm, of ♀ 4.3 (3.6–4.8) mm. Crown not strongly produced (median crown length 1.08 x interocular width, 0.57 x head width) (♂ n = 12; ♀ n = 21). Face entirely pale. Pronotum (Fig. 2A) traversed by six longitudinal stripes, central pair extending to rear of crown, across scutellum, and as spots on base of forewing; pair of transverse lines midway on crown. Forewings subhyaline with several highly pigmented cells, conspicuously pigmented, costal cross-veins, and conspicuous pigmentation along the inner edge of the forewing. [♂] Pygofer (Fig. 62Q) with posterior lobe short, with small, rounded, ventrally produced lobe. Plates (Fig. 8A) elongate, unnotched. Aedeagus symmetrical, gonopore subapical on caudoventral surface. Aedeagal apex (Fig. 7B) with pair of distinctive, bifurcate processes, each with few teeth on the dorsal margin. Apodemal processes greatly expanded at apex. [♀] Sternum VII (Fig. 10A) with posterior margin shallowly concave on each side of produced median portion. Ovipositor with base of each first valvula (Fig. 63O) recurved, basal extremity rounded and directed caudodorsad.

GEOGRAPHIC DISTRIBUTION.—This species occurs in the prairie of Minnesota and North Dakota, east to Illinois and south to the Blackland tall-grass prairie of Texas (Fig. 30).

BIOLOGY.—*Flexamia albida* is a resident of tall-grass and mixed prairies. Many records are from *Schizachyrium scoparium*. However, *albida* is not found in pure stands of *S. scoparium*, suggesting a life history more complex than that of other *Flexamia* species.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Panicoideae 0.674 (*Schizachyrium scoparium* 0.674); Chloridoideae 0.196 (*Bouteloua curtipendula* 0.196) (n = 46).

REMARKS AND DIAGNOSIS.—The habitus of *F. albida* is unique, and its geographic range does not overlap that of the other striped *Flexamia* species.

### 19. *Flexamia slossonae* (Ball)

*Deltocephalus slossoni* [sic] Ball 1905: 119.
*Deltocephalus (Flexamia) slossoni*, DeLong 1926: 36.
*Deltocephalus (Secopennis) slossoni*, DeLong and Sleesman 1929: 85.
*Flexamia slossoni*, DeLong and Caldwell 1937: 27.
*Secopennis slossonae*, Oman 1949: 168.

IMPORTANT CHARACTERS.—Length of ♂ 3.8 (3.5–4.2) mm, of ♀ 4.2 (3.8–4.5) mm. Crown produced (median crown length 1.38 x interocular width, 0.64 x head width) (♂ n = 20; ♀ n = 20). Face ivory with black interocular band at base. Dorsum with longitudinal lines extending from rear of the head across pronotum and scutellum to rear of forewings (Fig. 2B). Male plates (Fig. 8B) exceeding pygofer in length. [♂] Aedeagus (Fig. 7C) symmetrical, gonopore an elongate slit extending through most of length of unpaired ventral process; apical processes bifurcate, without teeth. [♀] Sternum VII (Fig. 10B) conspicuously tri-lobed.

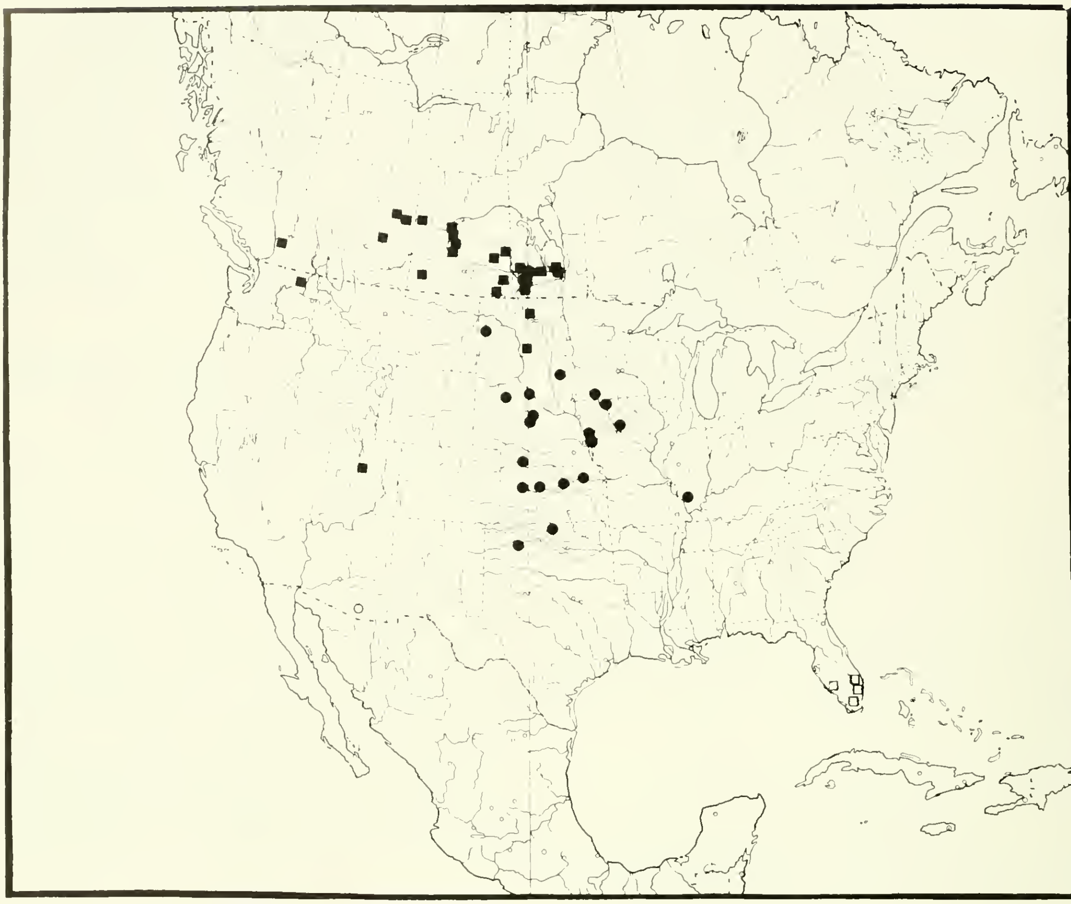

Fig. 30. Geographic distribution of *Flexamia serrata* (■), *albida* (●), *slossonae* (□), and *ritana* (○).

GEOGRAPHIC DISTRIBUTION.—*Flexamia slossonae* is restricted (Fig. 30) to subtropical grasslands of south Florida.

BIOLOGY.—DeLong (1926) reported finding adults and nymphs of *slossonae* on saltgrass (*Distichlis spicata*). We have found the species on the *Muhlenbergia* prairies of the Florida Everglades, in the absence of *Distichlis*. It seems likely that this species is a habitat rather than a host specialist.

REMARKS AND DIAGNOSIS.—Even if *slossonae* were not confined to the subtropical region of south Florida, its habitus would permit its unambiguous identification. The dorsal stripes of *albida* (Fig. 2A) are somewhat similar to those of *slossonae*, but in the latter species the stripes extend conspicuously to the rear of the forewings (Fig. 2B). Also, the forewings (Fig. 2B) are obliquely truncate, exposing the terminal abdominal segment, which is also striped. The forewings of *ritana* (Fig. 2D) are broadly truncate.

## VIII. The *ritana* Group

The *ritana* group consists of a single species. The monobasic group is defined by the bizarre aedeagal apex, which we designate as an autapomorphy.

### 20. *Flexamia ritana* Beamer

*Flexamia ritana* Beamer 1936: 257.

IMPORTANT CHARACTERS.—Length of ♂ 4.2 (3.9–4.4) mm, of ♀ 4.4 mm. Crown produced (mean crown length 1.67 x interocular width; 0.73 x head width) (♂ n = 4; ♀ n = 1). Dorsum

with stripes extending from head to forewings (Fig. 2D). Face pale white with broad, fuscous interocular band. [♂] Plates (Fig. 8D) about 1/2 length of pygofer, fused basally, tapering to bluntly acute apices. Aedeagus symmetrical, gonopore on caudoventral surface at base of unpaired processes (Fig. 7D); processes with entire edges, together lyriform; apodemal processes with anteapical protuberances. [♀] Sternum VII with conspicuous, median projection on hind margin.

GEOGRAPHIC DISTRIBUTION.—*Flexamia ritana* has been collected only in the Santa Rita Mountains of Arizona (Fig. 30).

BIOLOGY.—Despite many field hours expended in search, *ritana* has not been found since its collection in 1935. The original field notes of R. H. Beamer are not explicit in pinpointing the locality (see notes, Appendix III). Our field studies have emphasized collections on relatively pure patches of grass. Considering the accumulating evidence that primitive *Flexamia* species may be habitat specialists, future efforts should perhaps be directed at diverse habitats rather than single host species.

REMARKS AND DIAGNOSIS.—Superficially, *ritana* (Fig. 2D) resembles *albida* (Fig. 2A) but lacks transverse lines on the crown and has no darkly pigmented forewing cells. The forewings (Fig. 2D) are broadly truncate. The male plates and female sternum VII are entirely unlike those of either *slossonae* or *albida*.

## IX. The *serrata* Group

This group consists of a single species. The defining autapomorphy of the group is the pair of dorsal, aedeagal processes.

### 21. *Flexamia serrata* Beamer & Tuthill

*Flexamia serrata* Beamer & Tuthill 1934: 4.

IMPORTANT CHARACTERS.—Length of ♂ 3.9 (3.6–4.3) mm, of ♀ 3.8 (3.2–4.4) mm. Crown moderately produced (mean crown length 1.26 x interocular width, 0.66 x head width) (♂ n = 20; ♀ n = 20). Face pale with interocular band consisting of parallel lines interrupted at middle. [♂] Pygofer (Fig. 62P) with posterior margin of lobe subangulate above midlength. Plates (Fig. 8C) short, broadly triangulate, about half length of pygofer, acute at apices. Aedeagus (Fig. 7A) subsymmetrical, gonopore anteapical on caudoventral surface. Prominent, unpaired, ventral process basad of gonopore, extending basad along shaft, pair of shorter, recurved processes arising on each side of gonopore. Apodemal processes with mesal, anteapical protuberances. The unpaired aedeagal processes of some males from Linton, North Dakota (11 August 1977, 3 ♂, 3 ♀, R. F. Whitcomb, IPL 000351, and 24 July 1985, 34 ♂, 16 ♀, R. F. Whitcomb and E. A. Clark, IPL 001612) and Balta, North Dakota (1 ♂, 3 August 1985, K. G. A. Hamilton) are broken; such genitalia can be initially confusing. [♀] Sternum VII (Fig. 10C) with broad, median, posterior projection. Ovipositor with base of each first valvula very strongly recurved, recurved portion approximately parallel to axis of valvula (Fig. 63P).

GEOGRAPHIC DISTRIBUTION.—This species (Fig. 30) occurs from the southern tier of western Canadian provinces to Utah and North Dakota.

BIOLOGY.—*Flexamia serrata* is apparently associated with *Muhlenbergia richardsonis*, where it often occurs (especially in Canada) with *decora*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia richardsonis* 1.000 (n = 57).

REMARKS AND DIAGNOSIS.—The face pattern of *serrata* (Fig. 3A) is unique. The range of this species overlaps considerably with that of *stylata*, which has superficially similar facial lines. However, in *stylata* the lines are not interrupted at the middle and contrast with a yellow rather than white face. The male plates of *stylata* (Fig. 34E) and the unique morphology of the male pygofer (Fig. 5C) also differentiate it from *serrata*. Whereas all individuals of *stylata* have at least a trace of a transverse line midlength on the crown, *serrata* has a completely unmarked crown.

## X. The *flexulosa* Group

The *flexulosa* species group consists of 11 species. Evolution within this group has occurred on *Aristida*, *Bouteloua*, and, especially, *Muhlenbergia*. We have found no synapomorphy to define the group, but we have been able to define four subgroups. The nominate subgroup consists of two species. One of these, *arizonensis*, specializes on *Aristida purpurea* and/or other *Aristida* species. The other member of this subgroup is *flexulosa*, a

blue grama *(Bouteloua gracilis)* specialist. This species is designated as a sister to *arizonensis* on the basis of the extremely short, apically divergent plates, which are synapomorphic. The *decora* subgroup consists of three species. *F. decora* and *youngi* are identified as sisters on the basis of their ventral, aedeagal processes, which are much longer than the paired processes. Both are specialists on *Muhlenbergia richardsonis*. The current geographic distribution of these species suggests that they represent vicariant segregates of an ancestral *Muhlenbergia* specialist. The third species, *modica*, is a specialist on *Muhlenbergia repens* (a close relative of *M. richardsonis*) in more mesic grasslands of the eastern Desert Plains. This species is linked to the *decora* subgroup by the morphology of the male pygofer and female sternum VII. The third subgroup consists of three species: *arenicola*, a specialist on *Muhlenbergia pungens; stylata*, a specialist on *Muhlenbergia* species in uplands of the northern prairie and the eastern Rocky Mountains; and *celata*, a specialist of chloridoid grasses in sandhills, including sand blowout grass, *Redfieldia flexuosa*. The latter two species are designated sisters on the basis of their unique male pygofers, which are synapomorphic. A fourth subgroup consists of three species. One of these, *inflata*, a species of moist northern prairies, commonly occurs on *Muhlenbergia asperifolia*, which enables it to colonize riparian areas of the Southwest. *Flexamia texana*, a rare species from south central Texas whose biology is unknown, is designated sister to *beameri*, a species from New York whose biology is also unknown. The triangulate male plates and boat-shaped pygofers are synapomorphic for this subgroup.

### Description of the *flexulosa* Group

Small to large. Length of ♂ 2.9–4.6 mm, of ♀ 3.0–4.7 mm. Gray to stramineous. Crown not strongly produced in some species (*decora, inflata*), moderately produced in others. Face in many species (*flexulosa* and *decora* subgroups) white, ivory, or at the darkest, very pale yellow, contrasting sharply with dark, usually black interocular band. Face patterns in *stylata* subgroup similar, but with interocular band of parallel, discrete lines. In other species (*inflata* subgroup), face stramineous with no interocular band or at most indistinct band not contrasting with lower face. Male plates triangulate, short or elongate, often apically divergent, in some species fused basally. Aedeagus and connective articulated. Aedeagus with paired apical processes and ventral unpaired process in sagittal plane, or displaced from sagittal plane (*inflata* subgroup). Gonopore apical or subapical on caudoventral surface. Female sternum VII with median projection.

### Key to Males of the *flexulosa* Group

1. Pygofer produced caudally in spinelike process (Fig. 5C) .......... 2
— Pygofer not so .......... 3

2(1). Shaft of aedeagus thick, conspicuously curved, expanded apically with long, apical appendages (Fig. 31H) .......... *stylata* (Ball)
— Shaft of aedeagus slender, not conspicuously curved or expanded apically, with shorter apical appendages (Fig. 31I) ... *celata* Lowry & Blocker

3(1). Pygofer with posterior lobe produced, heavily sclerotized, and angled on ventral margin (Figs. 32E; 62MM) .......... *arizonensis* Young & Beirne
— Pygofer with posterior lobe rounded ventrally .. 4

4(3). Aedeagus with greatly elongate, unpaired ventral process *and* with shaft straight or arched caudodorsally .......... 5
— Aedeagus with paired and unpaired processes more or less same length *or* if one greatly elongate, then shaft sigmoidal .......... 6

5(4). Aedeagal shaft (Fig. 31G) curved, unpaired process straight .......... *decora* Beamer & Tuthill
— Aedeagal shaft (Figs. 31F, 38A,B) straight, unpaired process recurved .......... *youngi*, n. sp.

6(4). Aedeagal shaft at least weakly sigmoidal in lateral aspect .......... 7
— Aedeagal shaft arched caudodorsally, not sigmoidal .......... 9

7(6). Aedeagus with paired processes less than 1/4 length of unpaired process, and not diverging from plane of shaft in lateral aspect (Fig. 31E) .......... *inflata* (Osborn & Ball)
— Paired processes longer, and diverging from plane of shaft in lateral aspect .......... 8

8(7). Aedeagal processes irregular, apex strongly asymmetrical (Fig. 31A); south central Texas .......... *texana* Young & Beirne
— Aedeagal apex subsymmetrical (Fig. 31D), processes regular; New York .......... *beameri*, n. sp.

9(6). Pygofer in lateral aspect with caudoventral margin from ventral lobe to caudal apex straight, not curved; paired processes of the aedeagus in lateral aspect diverging dorsally from the plane of the shaft; dorsal keels of the connective narrow; plates (Fig. 33A) small, short ..... *flexulosa* (Ball)

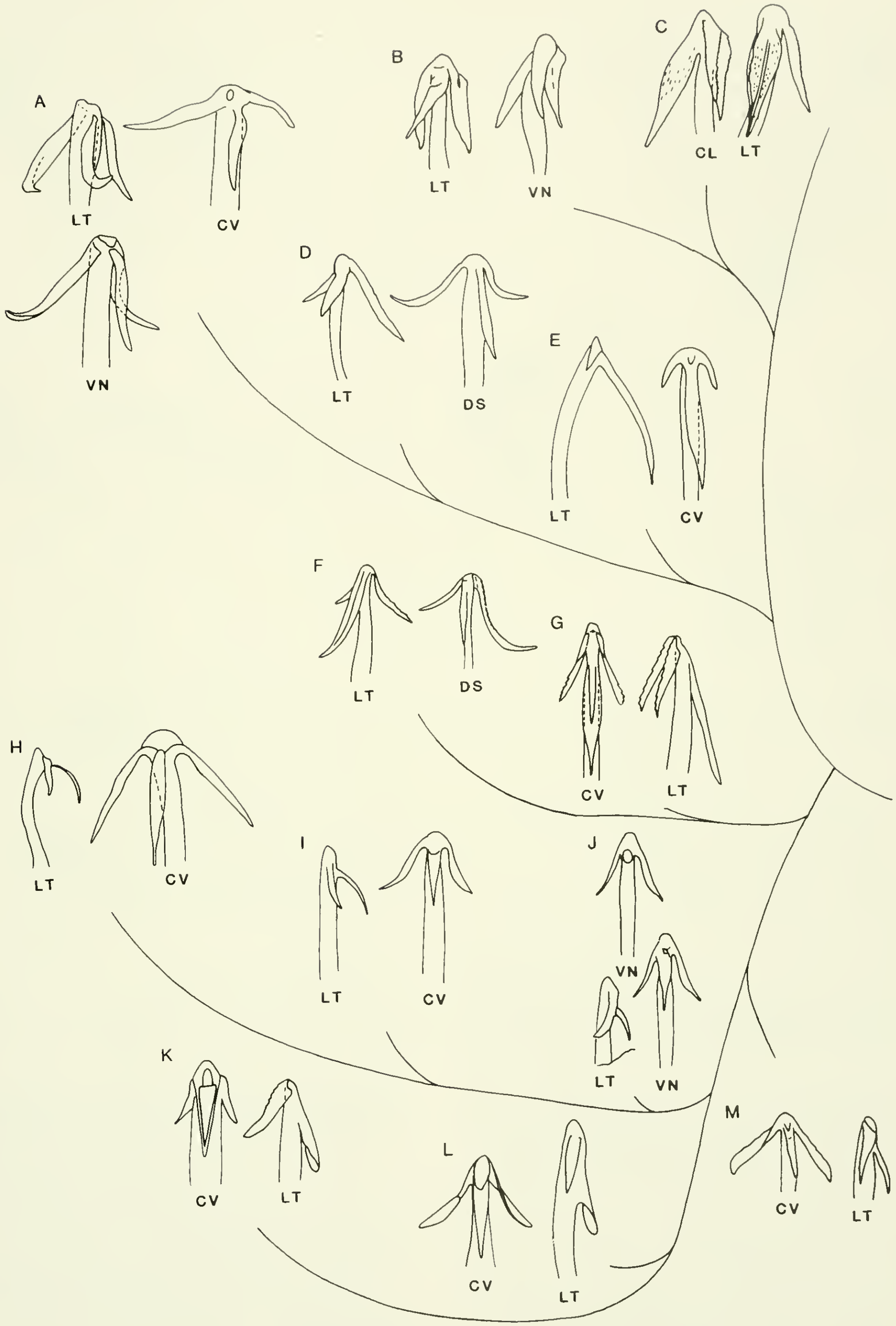


Fig. 31. Aedeagal apices of the *Flexamia flexulosa* group: A, *texana;* B, *imputans;* C, *areolata;* D, *beameri;* E, *inflata;* F, *youngi;* G, *decora;* H, *stylata;* I, *celata;* J, *arenicola;* K, *flexulosa;* L, *arizonensis;* M, *modica*. Aspects: CL, caudolateral; CV, caudoventral; DS, dorsal; LT, lateral; VN, ventral. Redrawn from Young and Beirne (1958).

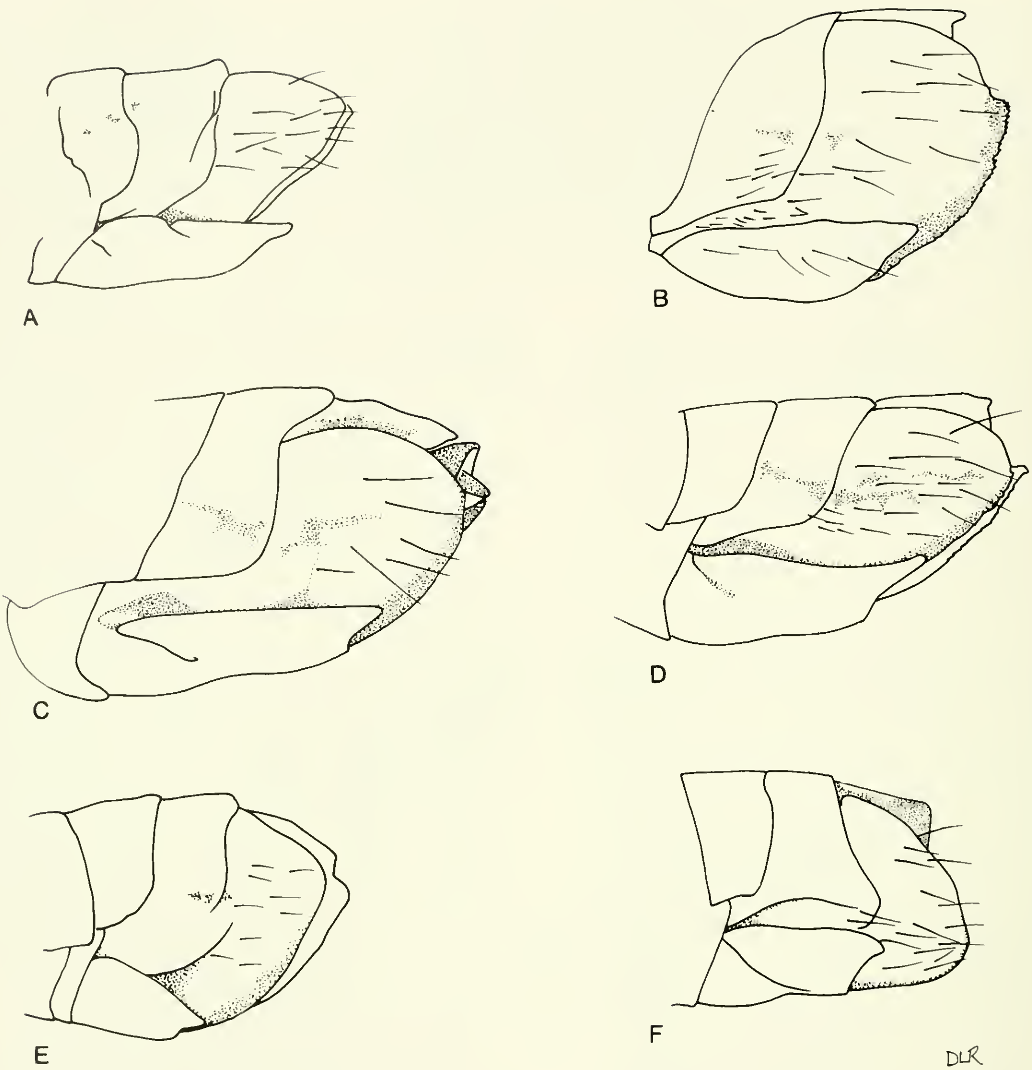


Fig. 32. Male plates and pygofers of some *flexulosa* group species, lateral aspect: A, *youngi*, B, *modica*, C, *arenicola*, D, *decora*, E, *arizonensis*, F, *flexulosa*.

— Pygofer in lateral aspect with caudoventral margin curved from ventral lobe to caudal apex; paired processes of aedeagus in lateral aspect diverging weakly or not at all from the plane of the shaft; dorsal keels wider in lateral aspect; plates (Figs. 33C,F) comparatively long . . . . . . . . . . . . . . . . . 10

10(9). Apices of paired processes curving ventrad in lateral aspect; processes and shaft of aedeagus comparatively robust . . . *modica* Beamer & Tuthill

— Apices of paired processes curving dorsad in lateral aspect; processes and shaft comparatively slender . . . . . . . . . . . . . *arenicola* Lowry & Blocker

Key to Females of the *flexulosa* Group

1. Ovipositor with base of each first valvula curved dorsad and laterad, forming angle of more than 45 degrees with long axis of valvula and extending laterad beyond lateral margin of valvula when viewed from above (Figs. 63Q,R,AA) . . . . 2

— Ovipositor with recurved portion of each first valvula not extending laterad beyond lateral margin of valvula (or only very slightly so); if longer than broad, then with long axis forming angle of less than 45 degrees with axis of valvula in dorsal aspect . . . . . . . . . . . . . . . . . . . . . . . . . . 4

2(1). Recurved base of each first valvula very slender in dorsal aspect, posterior margin concave (Fig. 63AA) . . . . . . . . . . . . . . . . . . . . . . . . . . *stylata* (Ball)

— Recurved base of each first valvula broader in

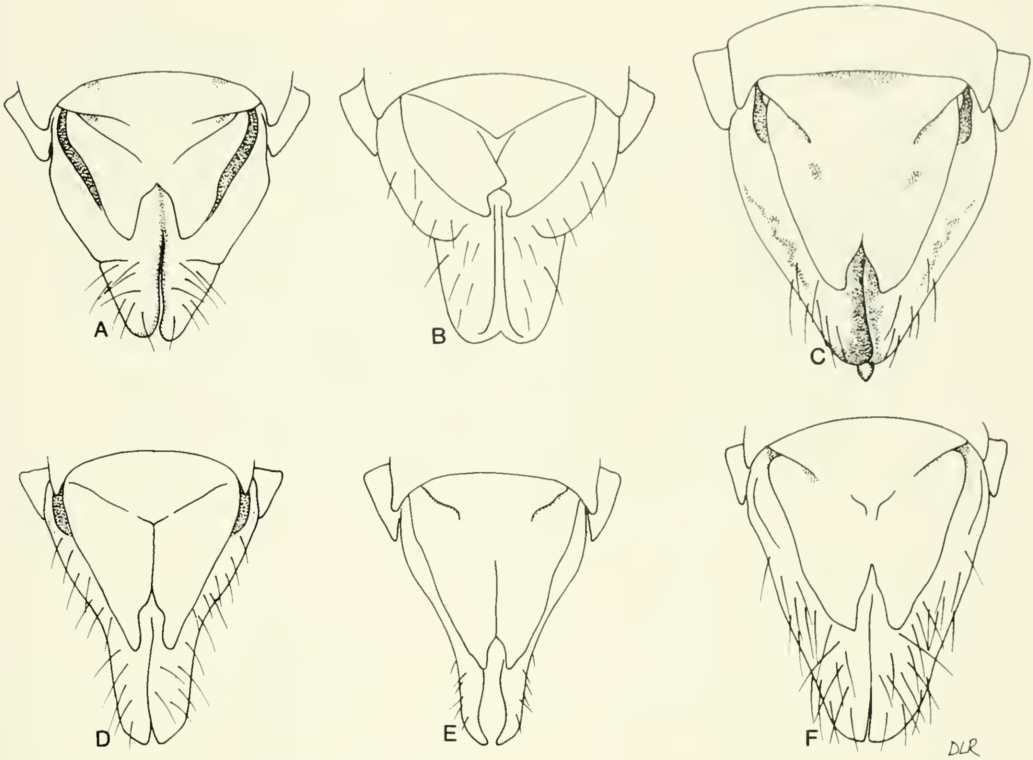


Fig. 33. Male plates and pygofers of the *Flexamia flexulosa* group: A, *flexulosa;* B, *arizonensis;* C, *arenicola;* D, *decora;* E, *youngi;* F, *modica.*

dorsal aspect, anterior margin straight or convex 3

3(2). Recurved base of each first valvula more distant from broadest part of valvula and with dorsal portion often lightly sclerotized and with small, anterior point (Fig. 63Q) .................... ........................ *decora* Beamer & Tuthill

— Recurved base of each first valvula without small, anterior point and closer to broadest part of valvula (Fig. 63R) ... *modica* Beamer & Tuthill

4(1). Recurved portion of each first valvula short, with acute, dorsal projection directed anterolaterad (Fig. 63T) .......... *inflata* (Osborn & Ball)

— Recurved portion of first valvula without such projection .................................. 5

5(4). Recurved portion of first valvula concave posteriorly in dorsal aspect (Fig. 63Y) ............ .................... *arizonensis* Young & Beirne

— Recurved portion of each first valvula not so ... 6

6(5). Recurved portion of each first valvula directed almost caudally (Fig. 63BB) ...... *flexulosa* (Ball)

— First valvula not so ........................ 7

7(6). Upper New York State .......... *beameri*, n. sp.

— South central Texas ...... *texana* Young & Beirne

## 22. *Flexamia arizonensis* Young & Beirne

*Flexamia arizonensis* Young & Beirne 1958: 30.

IMPORTANT CHARACTERS.—Length of ♂ 3.3 (3.0–3.8) mm, of ♀ 3.6 (3.2–4.0) mm. Head variably produced (1.40 x interocular width; 0.70 x head width) (♂ n = 20; ♀ n = 20). Face pale white with black interocular band. [♂] Pygofer with posterior lobe (Fig. 62MM) apically truncate, ventral portion extending ventrad as short, heavily sclerotized process. Plates short, less than 1/2 length of pygofer, apically divergent. Aedeagus symmetrical, paired apical processes arising on each side of subapical gonopore, unpaired ventral process about one-third length of shaft. [♀] Sternum VII with broad, median projection. Ovipositor with each first valvula (Fig. 63Y) curved at base more than 90 degrees, recurved portion concave caudally in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—This species is more widely distributed than had been previously supposed, occurring (Fig. 29) from

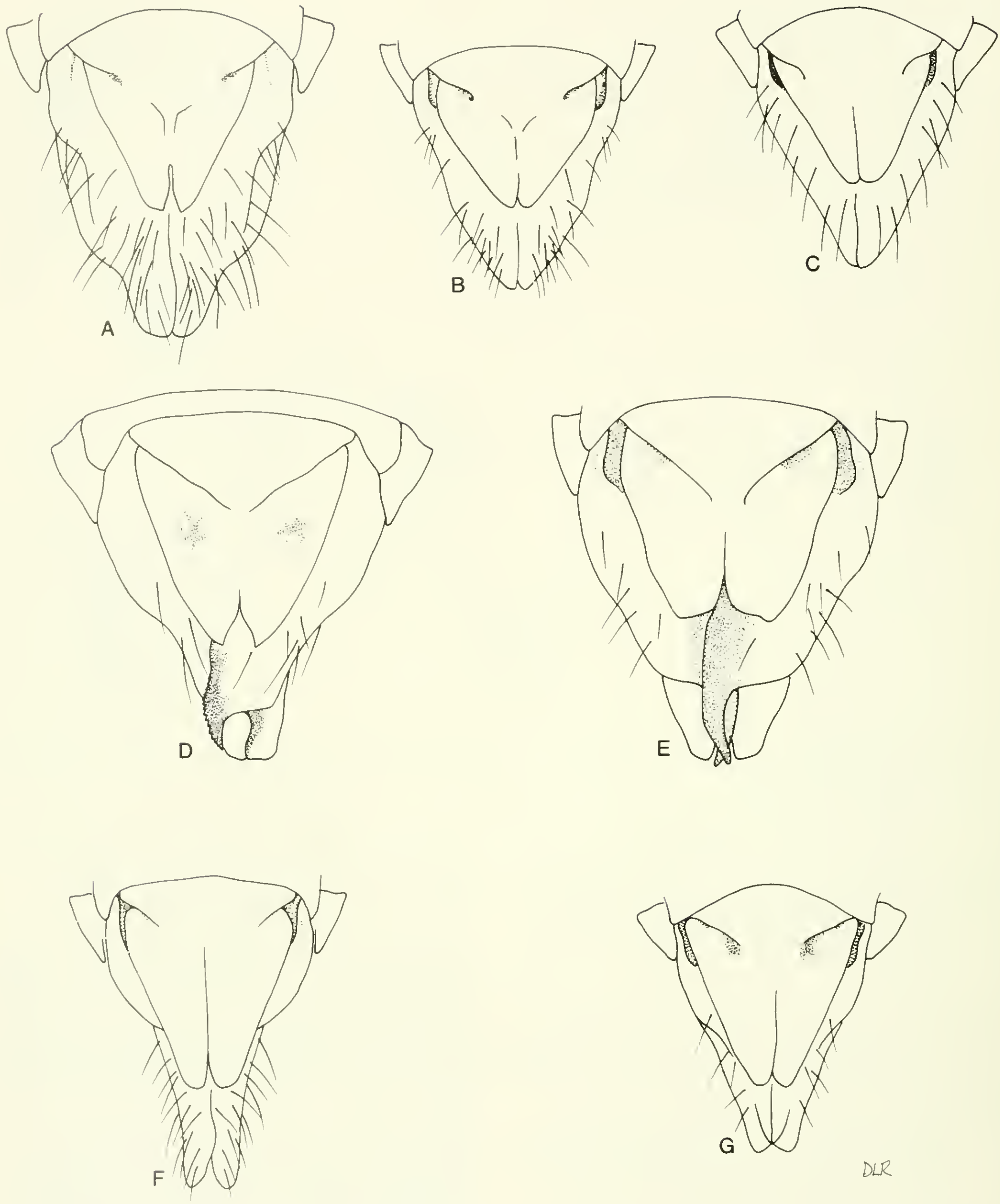


Fig. 34. Male plates and pygofers of the *Flexamia flexulosa*, *imputans*, and *areolata* groups, ventral aspect: A, *inflata;* B, *texana;* C, *beameri;* D, *celata;* E, *stylata;* F, *imputans;* G, *areolata.*

western Nebraska, Colorado, Utah, central Texas, and Arizona to northern Mexico (Sonora and Chihuahua). Two females from southern California (Pine Flats Camp, Indio, L. H. Banker, 12 July 1941 [KU]) may represent this species.

BIOLOGY.—This species is a specialist on perennial *Aristida* spp., especially *A. purpurea.*

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Aristida* spp. 0.932.

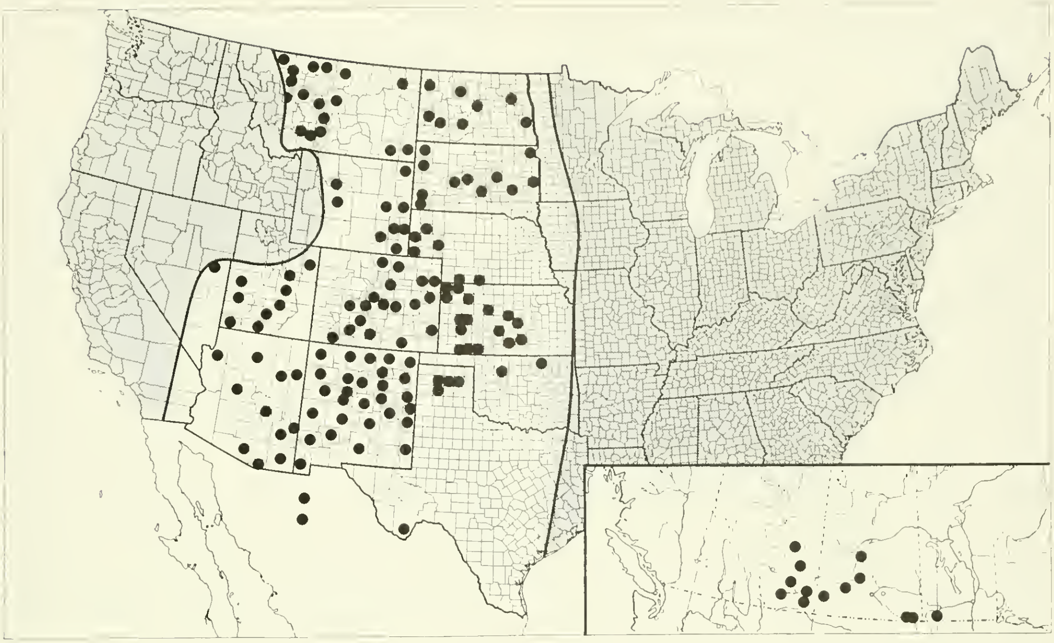

Fig. 35. Geographic distribution of *Flexamia flexulosa* and its host, *Bouteloua gracilis*.

REMARKS AND DIAGNOSIS.—Prior to the study of Young and Beirne, *arizonensis* had been confused with *flexulosa*. Males of these species can be distinguished by the lateral aspect of their undissected pygofers (Fig. 32E,F; see discussion under *flexulosa*). Although the dorsum of *arizonensis* is usually pale, several specimens from southern Arizona show dorsal stripes that are reminiscent of those of *ritana*. Since the external genitalic characteristics of *arizonensis* are very distinct from those of *ritana*, such specimens pose no problem for identification. However, they are important in suggesting an evolutionary link between the *ritana* and *flexulosa* groups.

### 23. *Flexamia flexulosa* (Ball)

*Deltocephalus flexulosus* Ball 1899: 189.
*Deltocephalus (Flexamia) flexulosus*, DeLong 1926: 31.
*Flexamius flexulosus*, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (2.9–3.7) mm, of ♀ 3.5 (3.0–4.1). Head variably produced (1.26 x interocular width; 0.60 x head width) (♂ n = 40; ♀ n = 44). Face pale with black interocular stripe. [♂] Pygofer (Fig. 62NN) with posterior lobe rounded apically. Plates very short, less than 1/2 length of pygofer, apically divergent. Aedeagus symmetrical, gonopore anteapical on caudoventral surface; paired apical processes short, minutely serrulate along one edge; unpaired ventral process short, grooved, less than one-fourth length of the shaft, acute at apex. [♀] Sternum VII with hind margin produced to form convex lobe; ovipositor with each first valvula curved through more than 90 degrees at base, recurved portion slender, almost parallel to long axis of valvula, with narrow projection extending caudad at basal extremity.

GEOGRAPHIC DISTRIBUTION.—This species occurs (Fig. 35) from eastern Nevada, Utah, Wyoming, Montana, and the southern tier of Canadian provinces from Alberta to Manitoba, south through the Great Plains to western Texas, Arizona, and northern Mexico (Chihuahua).

BIOLOGY.—Although *flexulosa* and *abbreviata* are both specialists of blue grama (*Bouteloua gracilis*), their ranges do not completely overlap. Whereas *flexulosa* appears to be adapted solely to blue grama in cool, dry climates, *abbreviata* is adapted to warmer grasslands, especially the mixed *Bouteloua*

grasslands of Texas, New Mexico, and Arizona. Such differences may be important clues to the evolutionary origins of these *Flexamia* species.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000, Chloridoideae 0.973; *Bouteloua gracilis* 0.889 (n = 380).

REMARKS AND DIAGNOSIS. — Young and Beirne (1958) consider *flexulosa* to be "greatly variable." Actually, we have found substantial variability in all *Flexamia* species for which large sample sizes were available; *flexulosa* seems to us to be no more or less variable than other species. The face pattern of *flexulosa* (black interocular band contrasting with a pale face) is, in fact, remarkably stable. Unfortunately, this contrasting pattern is shared by other members of the *flexulosa* group (*arizonensis*, *modica*, *arenicola*, *decora*, and *youngi*). Although the definitive identity of these species should be ascertained by examination of genitalic characteristics, *flexulosa* is an abundant species, so it is important to define external characters that permit it to be sorted from less common species. The lateral aspect of the male pygofer (Figs. 32A–F) is a useful character in sorting white-faced members of the *flexulosa* group. In *flexulosa* the posterior margin of uncleared male pygofers appears rounded. The pygofer (Fig. 32E) of the widely distributed *arizonensis* is truncate apically, but it is necessary to clear the specimen to see the distinctive, heavily sclerotized ventral process. In regions where both *decora* and *flexulosa* occur, *decora* can often be recognized by its characteristic habitus (see discussion under that species), and by its pygofer (Fig. 32D), which appears narrower than that of other white-faced species. The pygofer of *modica* (Fig. 32B), an uncommon but locally abundant (New Mexico mountains) specialist of *Muhlenbergia repens*, is also diagnostic. The pygofer of *arenicola* (Fig. 32C) is also more or less diagnostic; this insect is an inhabitant of *Muhlenbergia pungens* in the Nebraska Sand Hills and the Four Corners region of the Colorado Plateau (Fig. 36). Thus, the combination of male pygofer, geographic range, and host data (if available) provides an excellent character set that permits tentative recognition of pale-faced males of the *flexulosa* group. Nevertheless, the identity of these species, including *flexulosa*, should be confirmed by examination of characters of the genitalia.

24. *Flexamia arenicola* Lowry & Blocker

*Flexamia arenicola* Lowry & Blocker 1987: 59.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.5–3.9) mm (Sand Hills form), 3.4 (3.2–3.8) mm (Anasazi form); of ♀ 4.0 (3.8–4.3) mm (Sand Hills form), 3.7 (3.3–4.1) mm (Anasazi form). Crown moderately produced (median crown length 1.19 x [Sand Hills form] or 1.35 x [Anasazi form] interocular width; 0.63 x head width [both forms]) (♂ n = 20, ♀ n = 7 [Sand Hills form]; ♂ n = 20, ♀ n = 18 [Anasazi form]). Crown moderately produced (median crown length 1.25 x interocular width; 0.67 x head width). Face pale, with conspicuous, black interocular band. [♂] Pygofer (Fig. 62LL) broadly ovate; plates (Fig. 33C) broadly triangulate, diverging apically. Aedeagus (Fig. 31J) symmetrical with gonopore anteapical on the caudoventral surface, lateral, apical processes approximately one-fourth shaft length and curved laterodorsad; unpaired process approximately the same length and directed anteriorly. [♀] Sternum VII with posterior margin produced medially with small, median notch. Ovipositor with recurved process at base of first valvula (Fig. 63S) not exceeding lateral margin, process extending caudad, sinuate and digitate apically.

GEOGRAPHIC DISTRIBUTION.—There are two disjunct populations of *arenicola* (Fig. 36). One population occurs in the sandhills of western Nebraska and northeastern Colorado. The other population occurs in the Colorado Plateau and adjacent regions of New Mexico. The disjunct distribution of *arenicola* can be readily explained by the essentially disjunct distribution of its host (Fig. 36).

BIOLOGY.—*Flexamia arenicola* has been found almost exclusively on sandhill muhly, *Muhlenbergia pungens*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia pungens* 0.989 (n = 91).

REMARKS AND DIAGNOSIS.—The unpaired processes of the aedeagus in males of the Four Corners population (which we term the "Anasazi form" in honor of the pre-Columbian residents of the area) is uniformly absent, but on close inspection it can be seen to be broken; this presumably occurs during copulation. The occurrence of the Anasazi form is

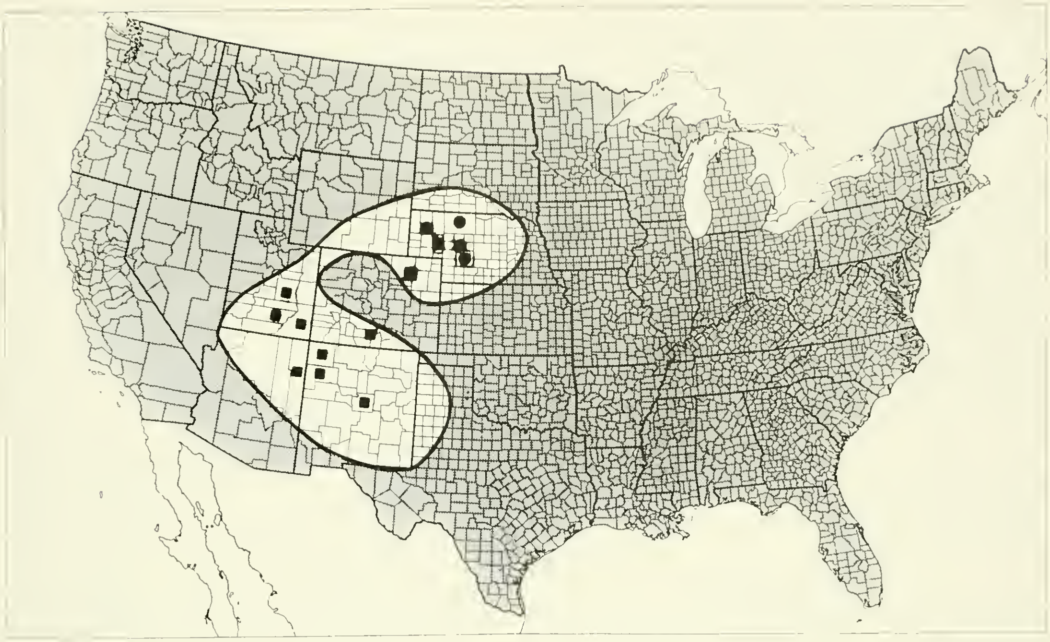

Fig. 36. Geographic distribution of *Flexamia arenicola* (Sand Hills [●] and "Anasazi" [■] forms) and the host, *Muhlenbergia pungens*.

patchy, and populations usually are low. Because the region occupied is now undergoing desertification and salinization as a result of climatic changes during the interglacial era, this form may be a relict population that, like the host population, is currently stressed by climatic change. Presumably, the outcome of these selective pressures could lead to extirpation or to evolution of a new species that would be better adapted to semiarid environments. The characteristics of the male pygofer (Fig. 32C) in lateral aspect, in combination with the face characteristics, are diagnostic for *arenicola*. Lowry and Blocker (1986) distinguished *arenicola* from *flexulosa* by the expanded dorsal keels of the *arenicola* connective, the more robust aedeagal shaft, and the longer aedeagal processes. They distinguished *arenicola* from *modica* by its larger size and nearly symmetrical aedeagus with lateral, dorsally curved, apical processes. In addition, the pygofer of *modica* (Fig. 32B) is very different from that of *arenicola*. Some characters in *arenicola* are similar to those of *celata* and *stylata*, but the general facies of the latter two species separate them from *arenicola*.

## 25. *Flexamia celata* Lowry & Blocker

*Flexamia celata* Lowry & Blocker 1987: 57.

IMPORTANT CHARACTERS.—Length of ♂ 4.1 (3.9–4.4) mm, of ♀ 4.5 (4.4–4.7) mm. Crown not produced (1.13 x interocular width; 0.58 x head width) (♂ n = 19; ♀ n = 6). Face, as in *stylata*, pale with broad interocular band consisting of parallel, discrete lines. [♂] Pygofer (Fig. 62PP) with central margin strongly produced to form spinelike process, as in *stylata*. Plates (Fig. 34D) extending to approximately 2/3 length of pygofer, fused mesally for 1/2 length, narrowed apically to rounded, lateral lobe, apices meeting in V-shaped notch. Aedeagus (Fig. 31I) symmetrical, shaft slender, neither conspicuously curved nor expanded apically, ventral and paired apical processes approximately equal in length and less than 1/4 length of shaft; gonopore apical on caudoventral surface. [♀] Sternum VII with posterior margin medially produced, with slight median notch; ovipositor with basal processes of first valvulae recurved and extending laterad beyond lateral margin.

GEOGRAPHICAL DISTRIBUTION.—Nebraska Sand Hills and southwestern Kansas (Fig. 37).

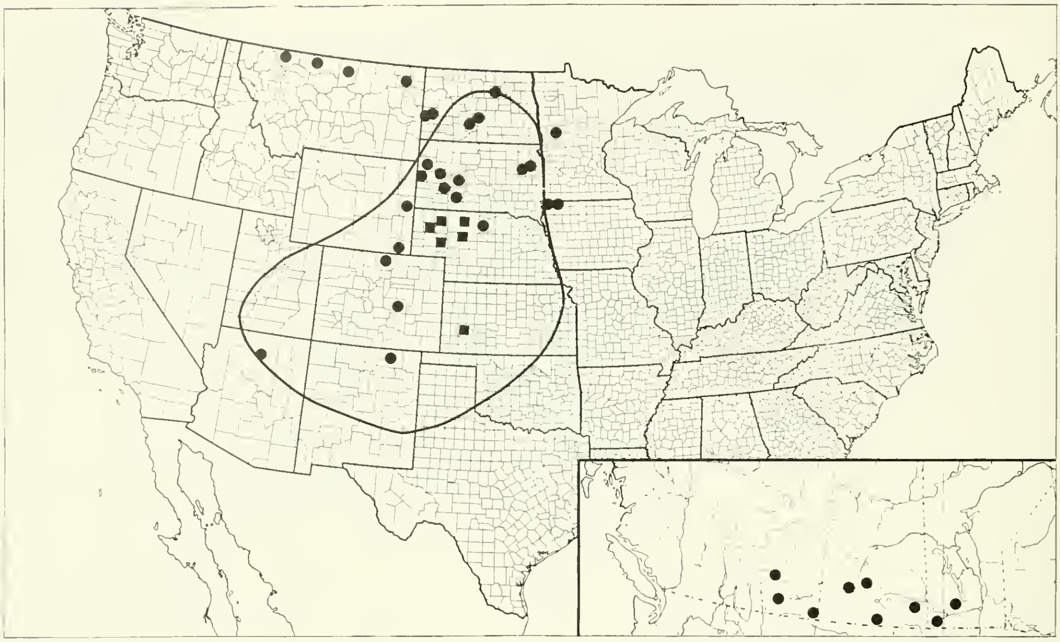

Fig. 37. Geographic distribution of *Flexamia stylata* (●) and *celata* (■) and a host of *celata*, *Redfieldia flexuosa*.

BIOLOGY.—This species occurs on sand blowout grass, *Redfieldia flexuosa*, the primary colonist of bare sand in the Sand Hills. It may also occur on other sandhill grasses. It has been recorded from *Calamovilfa longifolia* in southwestern Kansas (1 ♂, 3 ♀, Garden City, Finney County, 12 June 1948, R. H. Beamer).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; *Redfieldia flexuosa* 0.612; *Muhlenbergia pungens* 0.265 (n = 49).

DIAGNOSIS AND REMARKS.—This is a close sister species with *stylata*, under which diagnostic characters have been discussed. The present-day area of endemism was apparently created by the southern interface of the ice sheet during the last glacial maximum (Wright 1970), suggesting that *celata* could represent a recent speciation. On the other hand, its morphological characters are much closer to the ground plan for the *flexulosa* group than are those of *stylata*. The aedeagal symmetry and wide pygofer of *celata* suggest a relationship with *arenicola*, which occurs with it in the Nebraska Sand Hills.

## 26. *Flexamia stylata* (Ball)

*Deltocephalus stylatus* Ball 1899: 190.
*Deltocephalus (Flexamia) stylatus*, DeLong 1926: 34.
*Flexamius stylatus*, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 4.1 (3.7–4.6) mm, of ♀ 4.2 (3.8–4.6) mm. Crown not strongly produced (1.17 x interocular width; 0.54 x head width) (♂ n = 33; ♀ n = 33). Face pale, except for broad interocular band consisting of discrete, parallel lines. [♂] Plates (Fig. 34E) with conspicuous, subrectangular apices; pygofer (Fig. 62OO) with posterior margin strongly produced, gradually narrowed, forming curved, spinelike process. Aedeagus asymmetrical; shaft subcylindrical; gonopore subapical, at base of three processes on caudoventral surface; pair of apical processes directed laterobasad, unpaired ventral process extending basad to midlength of shaft, but not parallel to axis of shaft, the three processes appearing subequal in length in caudoventral aspect; paired processes appearing shorter in lateral aspect, each slightly serrate on dorsal edge. [♂] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63AA) curved dorsad through slightly more than 90 degrees, recurved portion extending laterad beyond lateral margin

of valvula in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Southern tier of Canadian provinces south through the western Great Plains, eastern Rocky Mountains, northern New Mexico, and Arizona (Fig. 37).

BIOLOGY.—This species has been collected from *Muhlenbergia* on upland slopes in Montana and Wyoming. In northern New Mexico the host is *Muhlenbergia wrightii*. This host may also account for records from northern Arizona.

DIAGNOSIS AND REMARKS.—The male plates of this species are unique. The face pattern (interocular bands with discrete lines) that *stylata* shares with *celata* is very distinctive; superficially similar species almost always have bands with coalesced lines. Finally, *stylata* specimens are larger than those of most other species. Females of *stylata* and *celata* are similar but can be distinguished by characteristics of the bases of the first valvula of the ovipositor. Also, *stylata* is a widely distributed *Muhlenbergia* specialist, whereas *celata* is restricted largely to the Nebraska Sand Hills, where it is a rare inhabitant of *Redfieldia flexuosa* and other chloridoid grasses.

### 27. *Flexamia decora* Beamer & Tuthill

*Flexamia decora* Beamer & Tuthill 1934: 2.

IMPORTANT CHARACTERS.—Length of ♂ 3.6 (3.0–4.2) mm, of ♀ 3.9 (3.4–4.2) mm. Head not strongly produced (median crown length 1.07 x interocular width, 0.62 x head width) (♂ n = 20; ♀ n = 20). Face pale with broad black interocular stripe. [♂] Pygofer (Fig. 62FF) with slightly truncate rear margin. Plates (Fig. 33D) broadly divergent, with narrow apices. Aedeagus (Fig. 31G) symmetrical. Gonopore anteapical on caudoventral surface; pair of retrorse processes arising on each side of gonopore, each serrate on dorsal edges. Unpaired ventral processes, with entire edges, extending basad more than half length of shaft. [♀] Sternum VII with hind margin concave at each side of median convex projection, notched apically, with teeth on each side of notch. Ovipositor with each first valvula (Fig. 63Q) with base expanded dorsally and laterally.

GEOGRAPHIC DISTRIBUTION.—*Flexamia decora*, as defined herein, is a specialist of *Muhlenbergia richardsonis* in the New Mexico and Colorado Rockies north to the Peace River region of northwestern Alberta, and east to Manitoba and North Dakota (Fig. 39). Its host occurs in eastern North America but does not occur south of Maine. We have examined specimens reported by Young and Beirne (1958) from Kentucky and Virginia. The Kentucky specimen is a female referable to *inflata*. The Virginia specimen labeled only "Oct. 12, Va., ED. Ball" appears to have been recently relabeled (and therefore possibly mislabeled), perhaps at the time of acquisition of the Ball collection. There are therefore no reliable records for *decora* east of the mixed-grass prairie.

BIOLOGY.—*Flexamia decora* appears to be largely a specialist of *Muhlenbergia richardsonis*. Large populations are not uncommon, and *decora* is the most abundant *Flexamia* species in the CNC (Appendix I).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.874; *Muhlenbergia richardsonis* 0.874. [Note: *M. richardsonis* has been present in all communities where *decora* occurs.]

REMARKS AND DIAGNOSIS.—Many individuals of *decora* have a rather distinctive habitus, with very dark forewing markings, especially on the apical portions, and along the veins of the forewing that contrast sharply with the lighter pronotum and crown. Unfortunately, paler specimens are not rare; the identity of these specimens is often indicated by the extremely short crown length. *Flexamia decora* and its close sister species, *youngi*, are apparently restricted to *Muhlenbergia richardsonis*.

### 28. *Flexamia youngi*, n. sp.

Length of ♂ 3.7 (3.4–3.9) mm, ♀ 3.8 (3.7–4.2) mm; head width of ♂ 1.12 mm, ♀ 1.18 mm. Crown not produced; median length of crown approximately 1.11 x head width and 0.58 x interocular width (♂ n = 16; ♀ n = 20).

Color stramineous. Crown with at most a trace of basal or midlength markings. Pronotum with or without traces of wide, brown stripes. Face with black interocular line contrasting with white lower face. Venter stramineous.

MALE.—Pygofer (Fig. 38D) as in *decora* but with posterior lobe less angulate, more

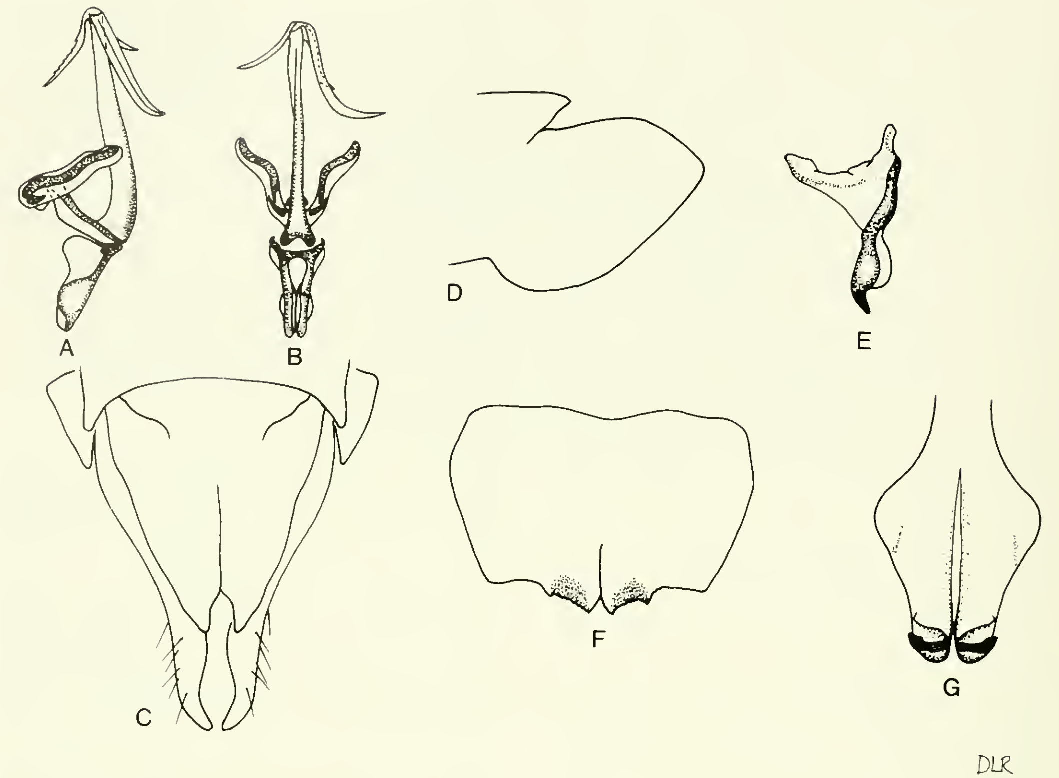


Fig. 38. *Flexamia youngi*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, male plates and pygofers, ventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, female sternum VII; G, bases of first valvulae of female, dorsal aspect.

broadly rounded ventrally; plates (Fig. 38C) extending approximately 2/3 length of pygofer, fused basally for 2/3 length, connective in lateral aspect (Fig. 38A) with dorsal keels broad, approximately 1/3 height of dorsal apodeme; apodemal processes sinuate in ventral view, bell-shaped in caudal aspect; styles as in other members of *decora* subgroup; aedeagus (Fig. 38B) asymmetrical, shaft elongate, apparently twisted 1/8 turn counterclockwise in caudal aspect, tapering gradually in lateral aspect, slightly enlarged apically in ventral aspect; three apical processes extending basad; unpaired process recurved, entire, with median ventral groove almost 1/2 length of shaft. Paired processes recurved, serrate on dorsal edges, approximately 1/3 length of unpaired process. Gonopore small, circular, and apical.

FEMALE.—Sternum VII (Fig. 38F) with posterior margin produced medially, pronounced median notch with infuscated spots on either side. Ovipositor with base of first valvula (Fig. 38G) recurved, appearing tear-shaped and only slightly exceeding lateral margins when viewed dorsally.

TYPES.—Holotype ♂: White Pine County, Nevada, Baker, 10 August 1986, R. F. Whitcomb (IPL 002590, *Muhlenbergia richardsonis*). Deposited USNM. Paratypes: 10 ♂, 11 ♀, same collection data; 1 ♀, Mt. Wheeler, White Pine County, Nevada, 10 August 1986, 8,500 ft, IPL 002569; 4 ♂, 4 ♀, Spring Valley, White Pine County, Nevada, 11 August 1986 (5,800 ft, R. F. Whitcomb, IPL 002596). Deposited in BARC, CNC, KSU, and USNM. Paratypes (KU) were also collected by R. H. Beamer (1 ♀, Deeth, Elko Co., Nevada, 21 July 1947); and D. H. Lindsay (1 ♂, 3 ♀ Soldier Summit, Utah, 13 August 1936).

REMARKS.—This species, apparently a Great Basin endemic (Fig. 39), is closely

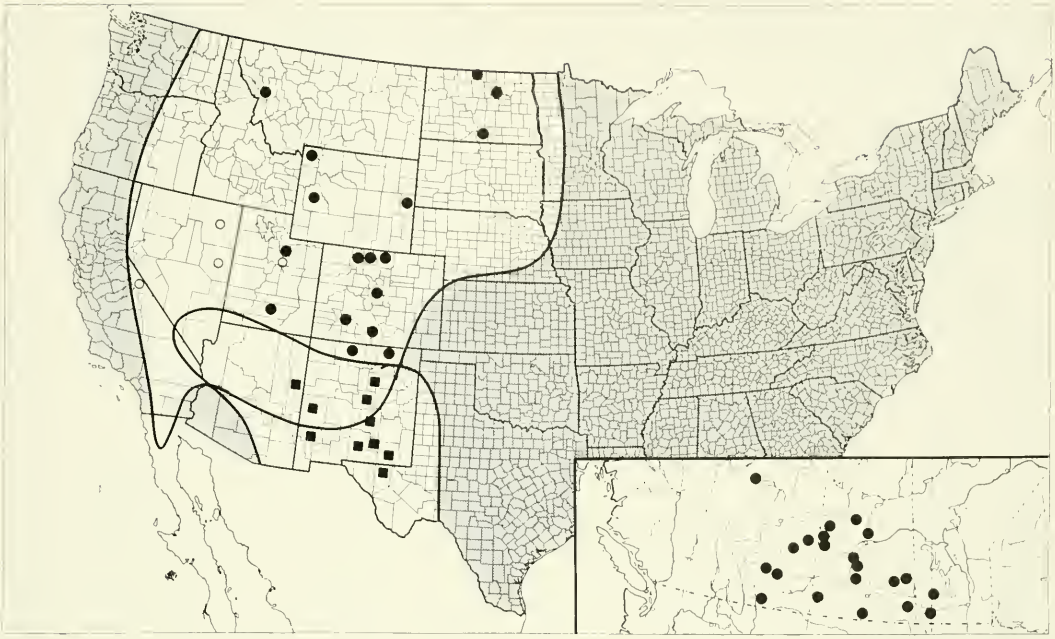

Fig. 39. Geographic distribution of *Flexamia decora* (●), *youngi* (○), and *modica* (■), and their hosts, *Muhlenbergia richardsonis (decora* and *youngi)* and *M. repens (modica)*.

related to *decora* but can be distinguished from it by the shape of the aedeagus, which is straight and twisted rather than curved and symmetrical, and by the recurved, apical processes. The host so far as known is (like *decora*) *Muhlenbergia richardsonis*. This species is named in honor of D. A. Young, whose classic monograph, with B. P. Beirne, established the modern generic concept of *Flexamia*.

29. *Flexamia modica* Beamer & Tuthill

*Flexamia modica* Beamer & Tuthill 1934: 3.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.1–3.7) mm, of ♀ 3.8 (3.4–4.0) mm. Crown moderately produced (1.26 x interocular width, 0.62 x head width) (♂ n = 20; ♀ n = 20). Face ivory, with broad interocular band. [♂] Pygofer (Fig. 62JJ) as in *decora*. Plates (Fig. 33F) short, about 2/3 length of pygofer, broadly triangulate, widely divergent at apices. Aedeagus (Fig. 31M) asymmetrical, gonopore triangular; unpaired ventral process less than half length of shaft, base appearing fused to shaft in lateral aspect. [♀] Sternum VII with broad median projection; ovipositor with base of each first valvula turned dorsad through 90 degrees and bilobed, recurved portion extending strongly laterad and exceeding lateral margin of valvula in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—High desert plains of southern New Mexico and adjacent counties of Trans-Pecos Texas and Arizona (Fig. 39). It is abundant in the Sacramento Mountains of southeastern New Mexico on its host *Muhlenbergia repens*. It is much less common in the Gila Mountains, where its host is more patchy, and occurs rarely in the central Guadalupe Mountains (Guadalupe Mountains National Park, Culberson Co., Texas) and northeastern Arizona (St. Johns, Apache Co.).

BIOLOGY.—Apparently a specialist of *Muhlenbergia repens*. Our records show seven series from this host 16–18 June 1985 (R. F. Whitcomb and K. A. Allred, approximately 440 ♂, ♀, and immatures). *M. repens* is closely related to *M. richardsonis* (Morden 1985, Morden and Hatch 1987). It is likely that *modica* arose from the *decora* lineage via

a host transfer from *M. richardsonis*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia repens* 1.000 (n = 377).

30. *Flexamia inflata* (Osborn & Ball)

*Deltocephalus inflatus* Osborn & Ball 1897: 202.
*Deltocephalus (Flexamia) inflatus*, DeLong 1926: 35.
*Flexamius inflatus*, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 3.8 (3.1–4.4) mm, of ♀ 4.0 (3.6–4.6) mm. Crown short (1.11 x interocular width; 0.58 x head width) (♂ n = 26; ♀ n = 26). Face stramineous, with or (more frequently) without a basal, pale brown interocular band. [♂] Pygofer (Fig. 62GG) with upper portion of posterior lobe strongly produced posteriorly. Plates (Fig. 34A) short, about 1/2 length of pygofer, apically divergent. Aedeagus (Fig. 31E) asymmetrical; shaft elongate, slender, gradually broadened apically; gonopore apical on caudoventral surface; pair of short, recurved processes arising on each side of gonopore, slender, unpaired ventral process almost half length of shaft, slightly expanded anteapically, acute at apex, which extends to right of shaft, all processes with edges entire. [♀] Female sternum VII broadly, medially produced, medially notched with traces of teeth between notch and lateral margin; ovipositor with base of each first valvula (Fig. 63T) curved dorsad, small projection on dorsal edge extending dorsolaterad, entire curved portion more heavily sclerotized and appearing almost as separate sclerite in ventrolateral aspect.

GEOGRAPHIC DISTRIBUTION.—This species is distributed (Fig. 41) from Utah, Texas, and New Mexico north to British Columbia and Manitoba east to Pennsylvania.

BIOLOGY.—This species may be adapted to northern mixed grasslands where pooid grasses, *Juncus* spp., and *Muhlenbergia* grow in intermixed stands. In the Southwest, at least, *inflata* is a specialist on *Muhlenbergia asperifolia*; occasional collections have also been made on *Distichlis spicata*. We do not have host records from the Northwest, but the northern limit of the distribution of *inflata* coincides roughly with that of *Muhlenbergia asperifolia*. In Illinois it occurs on *Juncus tenuis*. In Maryland it occurs on *Juncus tenuis* and on the introduced grasses *Cynodon dactylon*, *Zoysia japonica*, and *Eragrostis curvula*. This species has been reared on *J. tenuis* (Whitcomb 1957). Populations occasionally turn up for a time on *Festuca* or *Poa* but never seem to persist. We have observed no morphological indications of host races, although it is possible that the *Juncus* populations may be reproductively isolated from other populations. Rearing studies may be required to resolve the status of the biology of *inflata*.

OLIGOPHAGY COEFFICIENTS.—Prairie and savanna: Gramineae 0.725, Juncaceae 0.275; Chloridoideae 0.725, *Muhlenbergia asperifolia* 0.562; *Eragrostis curvula* 0.066 (n = 379). Other records: Manitoba (Woodside, 24 August 1981, 16 ♂, 16 ♀, *Poa pratensis*, K. G. A. Hamilton, CNC).

REMARKS AND DIAGNOSIS.—Although definitive identification of *inflata* requires examination of the genitalia, it is important to learn to sort the majority of specimens of this often abundant species on the basis of habitus alone. The vast majority of specimens of *inflata* are very lightly pigmented; these can be recognized by their light stramineous color in combination with a black spot on the apical forewing cell (Fig. 4A), by the lack of a spot in the corium, and by their crown, which is one of the shortest in the genus.

31. *Flexamia beameri*, n. sp.

Length of ♂ 3.2 (3.1–3.3) mm, ♀ 3.4 (3.3–3.4) mm; head width of ♂ 0.93 mm, ♀ 1.06 mm. Crown moderately produced; median length of crown 0.67 x head width and 1.39 x interocular width (♂ n = 6; ♀ n = 2).

Color stramineous with dark markings on corium and apical cell of forewings; face as in *inflata* and *texana;* head with light markings, pronotum with wide, faint stripes; venter and legs with irregular, fuscous markings.

MALE.—Pygofer (Fig. 40D) as in *texana;* plates extending to approximately 2/3 length of pygofer, fused basally for 3/4 length; connective in lateral aspect (Fig. 40A) with dorsal keels broad, approximately 2/3 height of dorsal apodeme; apodemal processes narrowly campanulate in caudal aspect; style (Fig. 40E) as in *inflata* and *texana;* aedeagus (Figs. 40A,B) slightly asymmetrical, shaft sigmoidal in lateral view, ventral unpaired process not quite in median plane of shaft and appearing slightly longer than strongly recurved, paired, lateral processes; all processes with edges entire; gonopore circular and apical.

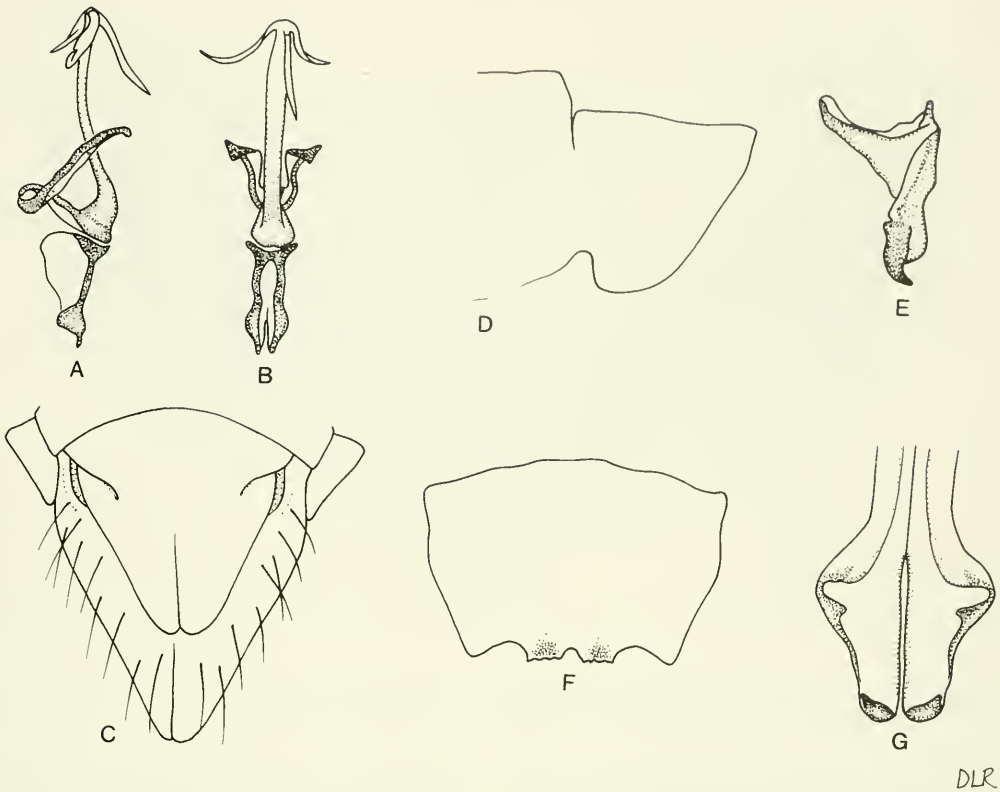


Fig. 40. *Flexamia beameri*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, male plates and pygofers, ventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, female sternum VII; G, bases of first valvulae of female, dorsal aspect.

FEMALE.—Sternum VII (Fig. 40F) similar or identical to *texana*, with median notched projection adjoined on each side by serrulate, infuscated projections; ovipositor with recurved portion of the bases of each first valvula (Fig. 40G) narrowing to diverging apices in dorsal aspect.

TYPES.—Holotype ♂: Otter Lake, Oneida County, New York, 25 June 1946, R. H. Beamer. Deposited KU. Paratypes: 5 ♂ and 2 ♀, same locality, deposited KU and USNM.

REMARKS.—This species, known from a single collection at its type locality (Fig. 41), is a sister to *texana*, a species also known from a single collection made long ago. *Flexamia beameri* can be readily separated from *inflata* and *texana* by the shape and length of the aedeagal processes. The aedeagal characters of *beameri* resemble those of *texana*, but the processes of *beameri* are not twisted. Presumably, the ranges of *beameri* and *texana* are very different. In contrast to the hot climate of south central Texas, the type locality of *beameri* is located in one of the coolest regions of New York (see Notes, Appendix III). Since we have not yet encountered these species in the field, their biology is a mystery. This species has been named in honor of R. H. Beamer, who described several interesting species of the genus and who collected the holotype and paratypes at a geographic site far from his home base.

## 32. *Flexamia texana* Young & Beirne

*Flexamia texana* Young & Beirne 1958: 29.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.9–3.2) mm, of ♀ 3.2 (3.0–3.5) mm. Crown not strongly produced (1.30 x interocular width, 0.63 x head width) (♂ n = 8; ♀ n = 2). [♂] Pygofer (Fig. 62HH) with upper margin flat in lateral aspect, posterior margin gradually rounded. Aedeagus

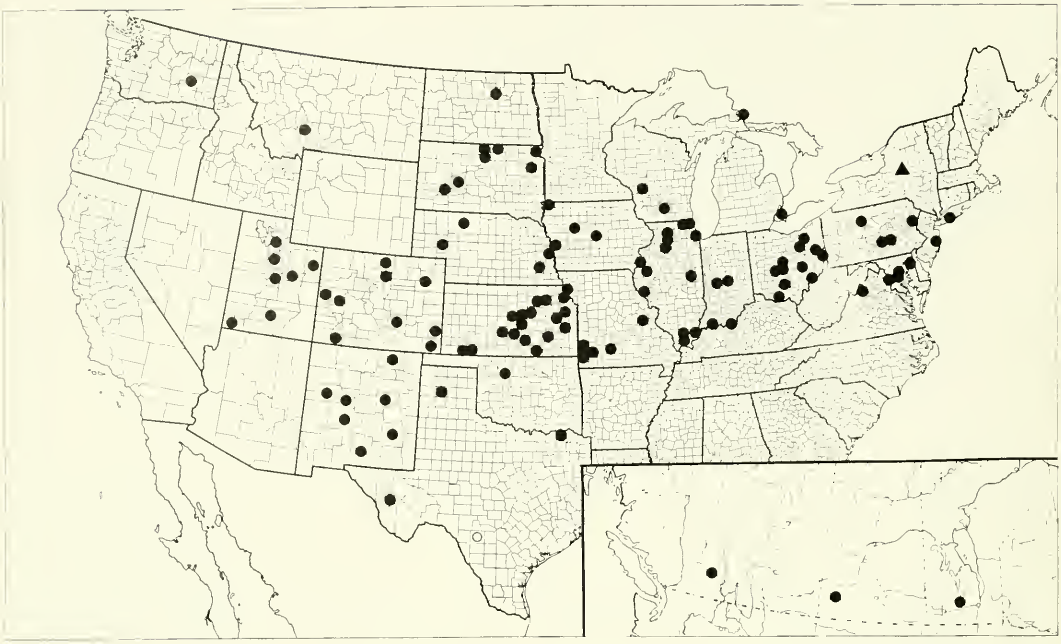

Fig. 41. Geographic distribution of *Flexamia inflata* (●), *beameri* (▲), and *texana* (○).

(Fig. 31A) asymmetrical; unpaired ventral and pair of lateral processes, all about equal in length, arising near gonopore; ventral process not in sagittal plane, lateral processes not in symmetrical planes. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63CC) curved dorsad through about 90 degrees in lateroventral aspect, base acute in lateral aspect, regularly convex in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Known only from the type locality (Uvalde, Texas).

BIOLOGY.—The host of *texana* is unknown. Uvalde is situated just south of the southern edge of the Edwards Plateau. We have surveyed the main, dominant, warm-season grasses of the Edwards Plateau searching for this species. Although these searches turned up a new species, *collorum*, they failed to locate *texana*. The grasslands of the mesquite-acacia savannah south of Uvalde have been largely plowed for agricultural crops. Perhaps E. D. Ball was afforded an opportunity to collect in these grasslands before they were sacrificed for agriculture. If this is the explanation for the rarity of this species, we may experience continuing difficulty in our search for this elusive species. On the other hand, discovery of the sister species *beameri*, whose type locality suggests a marshy wetland, raises the possibility that *texana* may turn up in wetlands in south Texas, which were overlooked in our searches.

## XI. The *imputans* Group

The *imputans* group consists of a single species, which is apparently a *Muhlenbergia* specialist in the northern prairie. This species retains the plesiomorphic articulation between connective and aedeagus; it could otherwise be regarded a close sister species to *areolata*, with which it shares a distinctive aedeagal morphology. These two species are both greenish dorsally and have black faces.

### 33. *Flexamia imputans* (Osborn & Ball)

*Deltocephalus imputans* Osborn & Ball 1898: 75.
*Deltocephalus (Flexamia) imputans*, DeLong 1926: 29.
*Flexamius* [sic] *imputans*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.1–3.7) mm, of ♀ 3.7 (3.3–3.9) mm. Crown moderately produced (1.33 x interocular width; 0.62 x head width) (♂ n = 10; ♀ n =

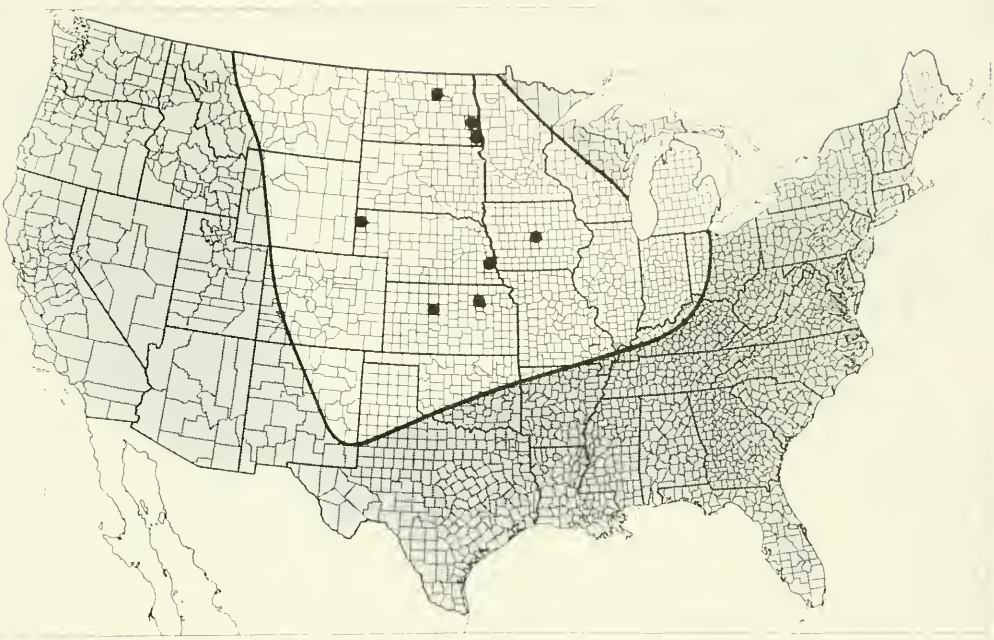

Fig. 42. Geographic distribution of *Flexamia imputans* and a probable host, *Muhlenbergia cuspidata*.

14). Face usually entirely black but occasionally with oblique, pale streak on each gena. [♂] Genitalia (Fig. 31B) similar to those of *areolata* but with hind margin of pygofer (Fig. 62V) convex and with distinct joint between connective and aedeagus. [♀] Sternum VII (Fig. 10P) with hind margin broadly, slightly convexly produced with slight median notch; ovipositor with bases of first valvulae (Fig. 63II) not recurved.

GEOGRAPHIC DISTRIBUTION.—Northern Great Plains from the Dakotas south to Kansas, east to Iowa and Wisconsin (Fig. 42).

BIOLOGY.—This species is apparently a *Muhlenbergia* specialist and may occur largely on *Muhlenbergia cuspidata*. It is one of the rarest of the *Flexamia* species and, given the extensive turnover of its original upland prairie habitat to croplands, may become increasingly rare.

REMARKS AND DIAGNOSIS.—This species is unique in its lack of markings on head and pronotum, in combination with its black face.

## XII. The *areolata* Group

This group consists of a single species.

### 34. *Flexamia areolata* (Ball)

*Deltocephalus areolatus* Ball 1899: 188.
*Deltocephalus (Flexamia) areolatus*, DeLong 1926: 25.
*Flexamia areolatus*, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 2.8 (2.6–3.2) mm, of ♀ 3.6 (3.2–4.0) mm. Crown strongly produced (1.77 x interocular width; 0.75 x head width) (♂ n = 20; ♀ n = 22). Face entirely black. [♂] Pygofer (Fig. 62Z) with dorsal portion of posterior lobe produced caudodorsad, posterior margin oblique and slightly concave. Plates (Fig. 34G) elongate, gradually narrowed from base to apex, fused basally for about 1/3 length. Aedeagus and connective fused. Aedeagus (Fig. 31C) asymmetrical; three tapering apical processes, two short, with serrate edges, extending basad along right side of shaft; third process extending basad for about half the length of right side of shaft, minute projections in middle, broader than other two processes, bearing gonopore as elongate slit through almost entire length. [♂] Sternum VII (Fig. 10Q) with posterior margin concave on each side of apically notched, median, convex projection; ovipositor with first valvulae not curved dorsad at bases.

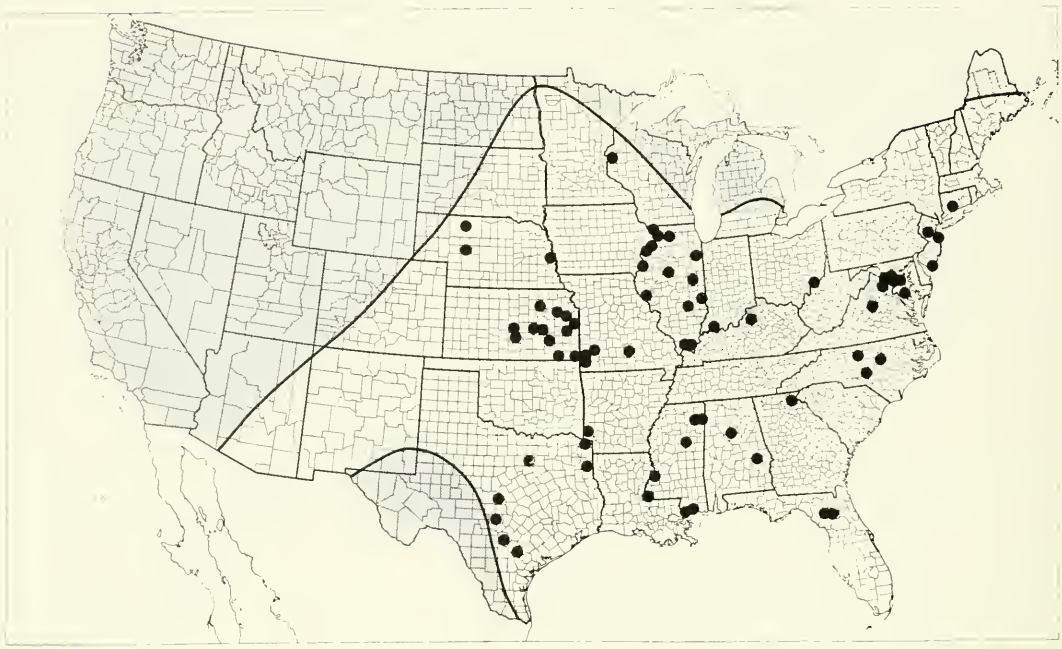

Fig. 43. Geographic distribution of *Flexamia areolata* and its host, *Eragrostis spectabilis*.

GEOGRAPHIC DISTRIBUTION.—This species occurs from Connecticut to Wisconsin, south to Florida and Texas, covering much of the geographic range of its host (Fig. 43). One of the three specimens from the original cotype series is labeled "Phoenix, Arizona, May, 1897." One specimen in the CNC is labeled "San Diego, Calif., 19-6-71, GL1251, H. H. Ross." Nevertheless, occurrence of *areolata* in the Southwest requires confirmation.

BIOLOGY.—We consider *areolata* to be a specialist of *Eragostis spectabilis*. DeLong (1949) believed that the host was "*Panicum* or a closely related genus." *Panicum capillare*, an annual that commonly occurs with *E. spectabilis* in sandy habitats, has a superficially similar inflorescence characterized by wide panicles that redden when mature. As if this were not confusing enough, *Leptoloma cognatum*, a representative of a genus that is indeed closely related to *Panicum*, not only occurs with the above two plant species in the same sandy habitats, but also has low, wide panicles that redden when mature. Unsure whether we may have overlooked components of this confusing plant association, we have returned to several communities where *areolata* occurs and have found *E. spectabilis* growing in the absence of the other two grasses. Furthermore, we have collected this species in the Nebraska Sand Hills on *E. spectabilis*, northwest of the range of *Leptoloma cognatum*. Osborn (1928) recorded *areolata* from *Eragrostis pectinacea* in North Carolina. Because *E. pectinacea* is an annual, this report requires confirmation.

REMARKS AND DIAGNOSIS.—The habitus of *areolata* is unique.

## XIV. The *prairiana* Group

The *prairiana* group is named for its most plesiomorphic member, *F. prairiana*, a widespread resident of tall-grass prairie and southwestern semiarid grasslands. The group consists of 10 species that share a similar general facies. All members of the group are medium-sized and brown but lack distinctive markings. Definitive identification requires examination of genitalia; the aedeagus and connective are fused, a condition we define as synapomorphic. In *prairiana* a trace of the plesiomorphic articulation remains and constitutes an autapomorphy defining that species. Species of this complex are largely

inhabitants of prairie, savanna, or forest glades. Members of the group specialize largely on andropogonoid grasses (*Andropogon*, *Schizachyrium*, and *Bothriochloa* spp.). Exceptions are (1) *atlantica*, which is often associated with switchgrass (*Panicum virgatum*) or, in the Southwest, chloridoid grasses such as *Sporobolus* spp.; and (2) *producta*, a southern coastal species that appears to be associated with chloridoid grasses. Both *atlantica* and *producta* regularly colonize an introduced chloridoid grass, *Cynodon dactylon*.

There are two sets of closely related sister species. One is *sandersi-delongi*. Ross and Cooley (1969) separated *delongi* from *sandersi* on the basis of the greater divergence of its apical, paired processes and lesser appression of the unpaired process to the aedeagal shaft (Figs. 44B,C). Hamilton and Ross separated *satilla* from *clayi* on the basis of a narrower aedeagal shaft (Figs. 44H,J). The distinctions between the species of these two sets are fine; some workers would consider the differences to represent infraspecific geographic variation. However, we have retained *satilla* and *delongi* because, in each case, they can be unambiguously identified, and a geographic and historical basis can be presented to explain both their divergence and maintenance of reproductive isolation. In the case of *delongi*, which probably specializes on *Schizachyrium scoparium*, the geographic range (Fig. 50) was almost entirely glaciated during the most recent glacial maximum. In contrast, *sandersi* occupies a region that was never glaciated, where it apparently specializes largely on *Andropogon virginicus*. These circumstances provide a hypothetical scenario for speciation and an explanation of ecological factors that may now enforce isolation between the two species. Similarly, *satilla*, described by Hamilton and Ross (1975) from south Georgia, is probably a Gulf Coast species (Fig. 51) that is at least partially sympatric with *producta*. Discovery of its sister species, *clayi*, as far north as Maine suggests that differentiation of these species, like that of *sandersi* and *delongi*, may be a postglaciation event that is phenologically enforced by contemporary climate. As closely related as *clayi* and *satilla* are, the sister set that they comprise is also very closely related to *graminea*. A more distant pair of sister species is that of *prairiana* and *reflexa*. The most significant apomorphy shared by these sister species is the dorsal position of the gonopore (Figs. 44D,G). These species also share a common general facies and cannot be distinguished on the basis of external characters. Each of these sister species has a variable aedeagal morphology, and we found that careful study was required to separate them. Both species are residents of tall-grass prairie, where they occur on *Andropogon* and *Schizachyrium* species. Other species of the *prairiana* group are more distantly related.

### Description of *prairiana* Group

Medium-sized. Length of ♂ 3.0–4.2 mm, of ♀ 3.0–4.6 mm. All species with similar general facies. Brown, or in darkest specimens, black on face or venter. Vertex moderately produced. Crown often stramineous with conspicuous transverse line at midlength. Male plates elongate, in some species notched apically. Aedeagus and connective fused, or with at most (in *prairiana*) a faint trace of the plesiomorphic articulation. Aedeagus with paired, apical, serrate processes and an unpaired, lateral or dorsal process partially fused to shaft in some species, or in others entirely fused or absent. Aedeagus asymmetrical in all but one species (*dakota*). Gonopore in primitive species oval and anteapical, in more advanced species located on the unpaired process or, in the most highly specialized species, replacing the unpaired process as a spiral groove originating dorsally on the shaft. Female sternum VII produced posteriorly at middle in a convex, apically notched protuberance.

#### Key to Males of the *prairiana* Group

| | | |
|---|---|---|
| 1. | Aedeagus with 3 processes on shaft | 2 |
| — | Aedeagus with 2 processes on shaft | 6 |
| 2(1). | Pygofer with posterior lobe strongly expanded on ventral margin (Fig. 5D) | *producta* (Walker) |
| — | Pygofer with ventral margin of posterior lobe not strongly expanded | 3 |
| 3(2). | Gonopore dorsal, anteapical, located on a process or at the base of one (Figs. 44D,G) | 4 |
| — | Gonopore on dorsolateral surface of shaft at base of retrorse process | 5 |
| 4(3). | Gonopore near apex of aedeagal shaft, at base of a process (Fig. 44G) | *prairiana* DeLong |
| — | Gonopore located on a process (Fig. 44D) | *reflexa* (Osborn & Ball) |

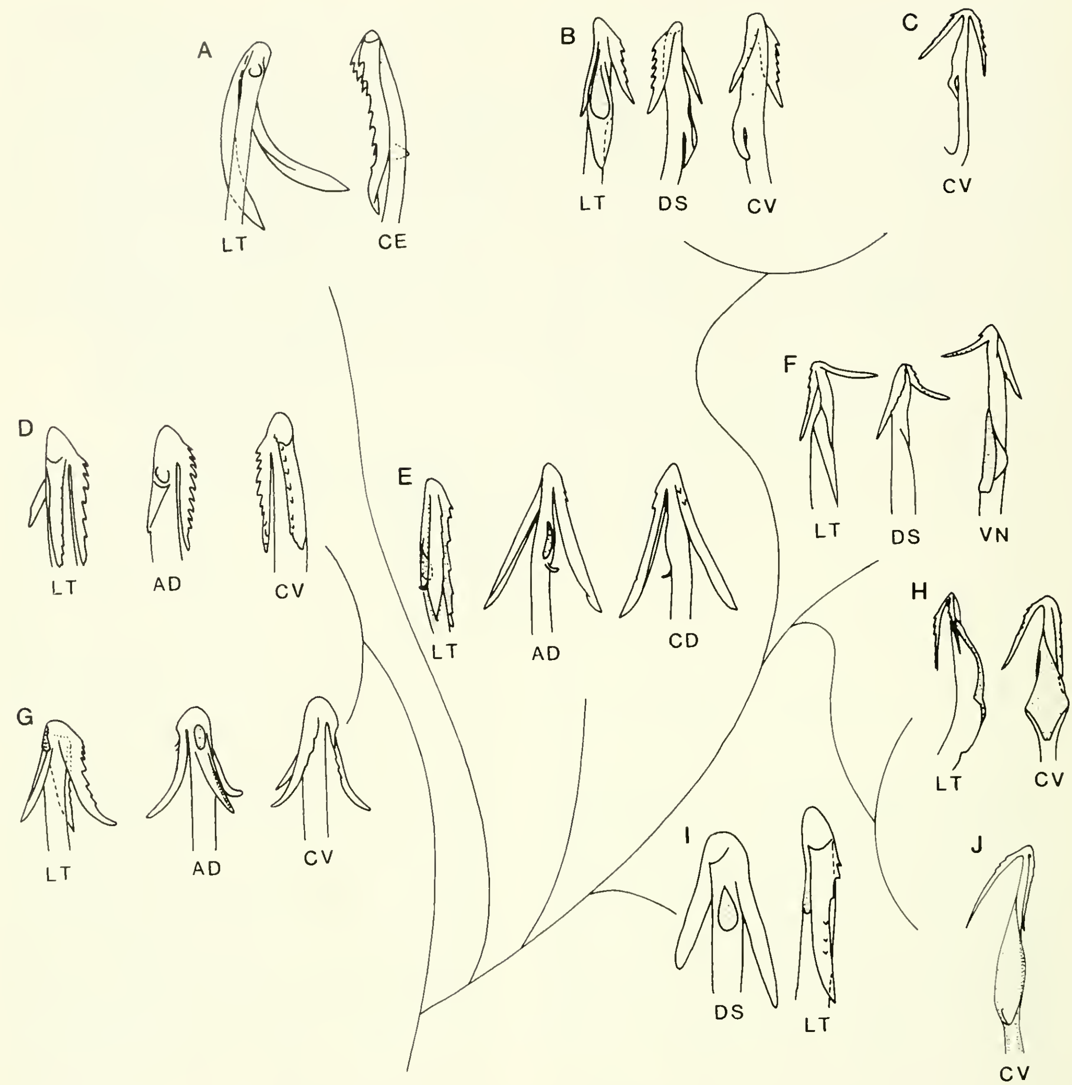


Fig. 44. Aedeagal apices of the *Flexamia prairiana* group: A, *atlantica;* B, *sandersi;* C, *delongi;* D, *reflexa;* E, *producta;* F, *graminea;* G, *prairiana;* H, *clayi;* I, *dakota;* J, *satilla*. Aspects: AD, anterodorsal; CD, caudodorsal; CE, cephalic; CV, caudoventral; DS, dorsal; LT, lateral; VN, ventral. Redrawn from Young and Beirne (1958) and Hamilton and Ross (1975).

5(3). Apical processes of aedeagus more divergent, each with 6–9 teeth; when viewed in a position with apical processes horizontal, a space is visible between the base of the gonopore extension and the shaft (Fig. 44C) . . . *delongi* Ross & Cooley

— Apical process of aedeagus less divergent, each with 3–5 teeth; when viewed as above, no space is visible between the base of the gonopore extension and the shaft (Fig. 44B) . . . . . . . . . . . . . *sandersi* (Osborn)

6(1). Gonopore spiral . . . . . . . . . . . . . . . . . . . . . . . . . . 7

— Gonopore not spiral . . . . . . . . . . . . . . . . . . . . . . . 8

7(6). Aedeagal appendages of aedeagus without prominent, anteapical processes; aedeagal shaft usually not strongly expanded at base of gonopore (Fig. 44F) . . . . . . . . *graminea* (DeLong)

— Apodemal appendages of aedeagus each with prominent, anteapical protuberance directed mesad; aedeagal shaft strongly expanded at base of gonopore (Fig. 44H) . . . . . . . . . . . . . . . . . . . . . 9

8(6). Aedeagal shaft with apical process on each side; gonopore anteapical on anterodorsal surface (Fig. 44I) . . . . . . . . . . . . . . *dakota* Young & Beirne

— Aedeagal shaft with apical processes arising on

one side; gonopore anteapical on lateral surface of shaft (Fig. 44A) ........... *atlantica* DeLong

9(7). Shaft of aedeagus comparatively robust (Fig. 44H); north Georgia to Maine ........................................ *clayi* Young & Beirne

— Shaft of aedeagus slender (Fig. 44J); Gulf Coast (Florida, south Georgia, Mississippi) ........................................ *satilla* Hamilton & Ross

Key to Females of the *prairiana* Group

1. Ovipositor with base of each first valvula recurved dorsally in dorsal aspect .............. 2

— Ovipositor with base of each first valvula not recurved dorsally .......................... 5

2(1). Recurved portion of each first valvula parallel to anteriormost border of each valvula in dorsal aspect, appearing as rim above the valvula (Fig. 63LL) .................................. 3

— Recurved portion appearing wider in dorsal aspect ....................... *prairiana* DeLong

3(2). Anteriormost border of each first valvula appearing somewhat angular in dorsal aspect, recurved portion very narrow and not produced dorsad (Fig. 63LL) .......... *graminea* DeLong

— Anteriormost border of each first valvula rounded, recurved portion much broader and produced dorsad (Fig. 63GG) ............... 4

4(3). Range north Georgia to Maine ........................................ *clayi* Young & Beirne

— Range Gulf Coast ....... *satilla* Hamilton & Ross

5(1). Bases of first valvulae obliquely truncate, valvulae apparently membranous basally (Fig. 63HH) ........................ *reflexa* (Osborn & Ball)

— Bases of first valvulae convex basally .......... 6

6(5). First valvulae broadest near bases in dorsal aspect (Fig. 63EE, KK) ....................... 7

— First valvulae broadest more posteriorly in dorsal aspect ................................ 8

7(6). Face often with brown interocular line contrasting with pale color of remainder; if without line, then irregularly darkened; Southeast (Fig. 49) .......................... *producta* (Walker)

— Face tan to dark brown with alternating sinuate, dark and light lines; dry prairie (Fig. 49) ...... ....................... *dakota* Young & Beirne

8(6). Face with black interocular line, or at least with this area black in addition to other black marks on face ..................... *atlantica* DeLong

— Face brown or tan; interocular area never black 9

9(8). Range southern Illinois southeastward ....... ............................ *sandersi* (Osborn)

— Range northern Illinois northward to Ontario, northwest to North Dakota ........................................ *delongi* Ross & Cooley

## 35. *Flexamia prairiana* DeLong

*Flexamia prairiana* DeLong 1937: 32.

IMPORTANT CHARACTERS.—Length of ♂ 3.6 (3.2–3.9) mm, of ♀ 3.9 (3.4–4.6). Crown moderately produced (0.60 x head width, 1.40 x interocular width) (♂ n = 73; ♀ n = 32). Face (Fig. 3D) usually pale in lower half, with broad, black interocular band; in darkly marked specimens almost completely black (Fig. 3C). Habitus characteristic of group. Male plates (Fig. 45A) elongate, unnotched. [♂] Pygofer (Fig. 62W) with upper part of hind margin produced posteriorly. Aedeagus (Figs. 6F, 44G) asymmetrical, shaft slender, elongate, gradually broadened apically; gonopore oval, anteapical on anterodorsal surface. Three retrorse apical processes diverging slightly from shaft, about one-third length of shaft. Unpaired process arising basad of gonopore, margins entire with dorsal, longitudinal groove on apical half; pair of distad, ventral, lateral processes, serrate on ventral margin. [♀] Sternum VII as for group; ovipositor with each first valvula (Fig. 63JJ) recurved slightly dorsad at base.

GEOGRAPHIC DISTRIBUTION.—Widely distributed (Fig. 46) from Manitoba to Colorado, Arizona, and Mexico, east to Missouri and Illinois. Two females from Michoacán, Mexico (21 October 1981, M. W. Nielson), have been tentatively referred to *prairiana*. A single male (Baker 2361, USNM) is recorded from Auburn, Alabama, 10 September 1897.

BIOLOGY.—Southwestern populations usually occur on *Bothriochloa* species. In the tall-grass prairie the usual hosts are *Schizachyrium scoparium* and *Andropogon gerardii*. Most reported hosts are andropogonoid grasses, but in tall-grass prairie *prairiana* may move short distances to more suitable hosts in drought periods or in late summer. Thus, oligophagy coefficients calculated for *prairiana* tend to be among the lowest for all *Flexamia* species (Whitcomb et al. 1988). The green coloration of live specimens of *prairiana* fades to orange upon drying. In midsummer the intensity of coloration varies greatly. In the fall, coloration may be very dark; uncleared, late-season specimens have often been misidentified.

OLIGOPHAGY COEFFICIENTS.—Tall-grass and mixed-grass prairies north of Texas: Gramineae 0.922; Panicoideae 0.730; *Schizachyrium scoparium* 0.438; *Andropogon gerardii* 0.241 (n = 527).

REMARKS AND DIAGNOSIS.—Because this species is one of the most abundant of *Flexamia* species, it is important to recognize it

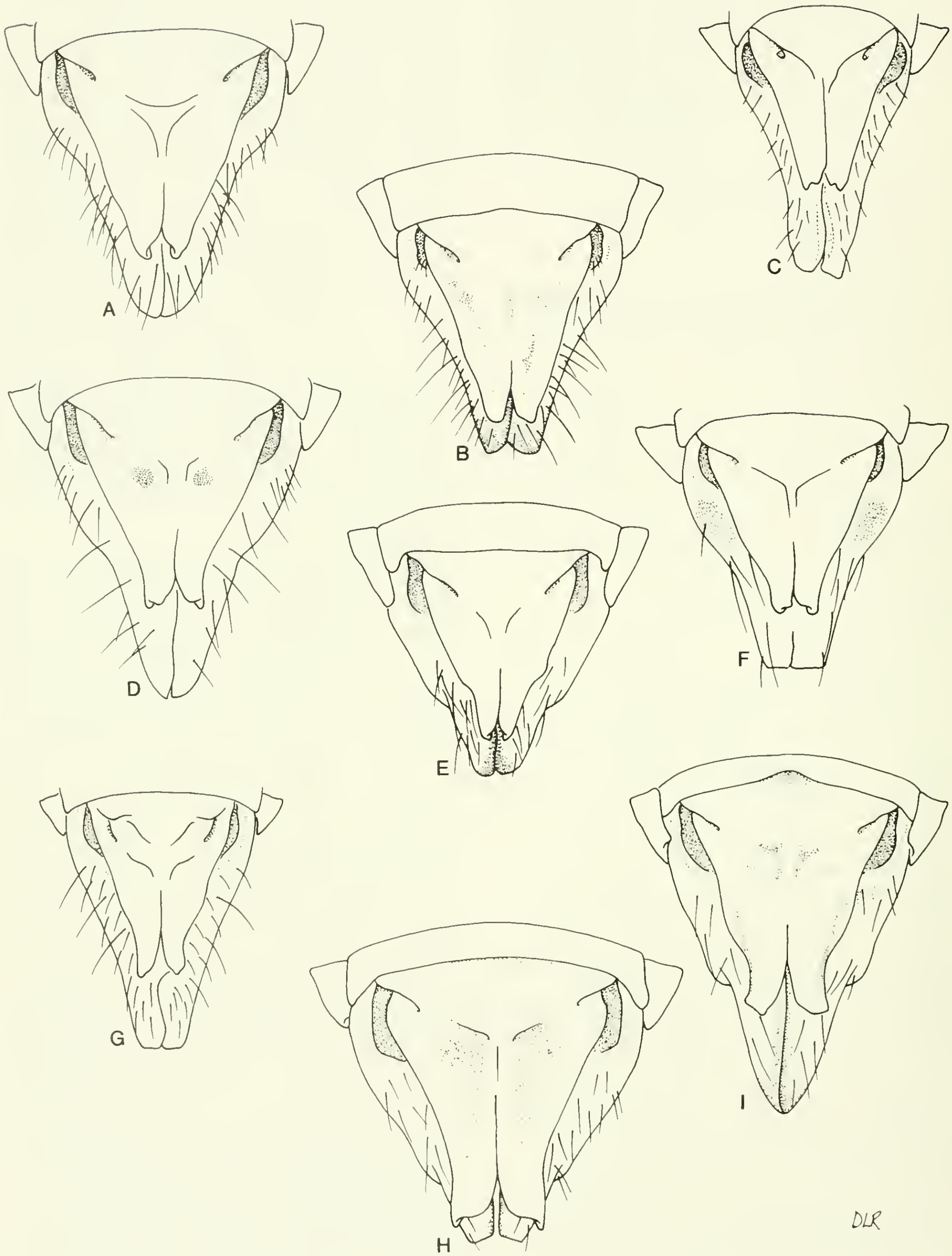


Fig. 45. Male plates and pygofers of the *Flexamia prairiana* group, ventral aspect: A, *prairiana;* B, *reflexa;* C, *atlantica;* D, *producta;* E, *dakota;* F, *sandersi;* G, *delongi;* H, *graminea;* I, *clayi.*

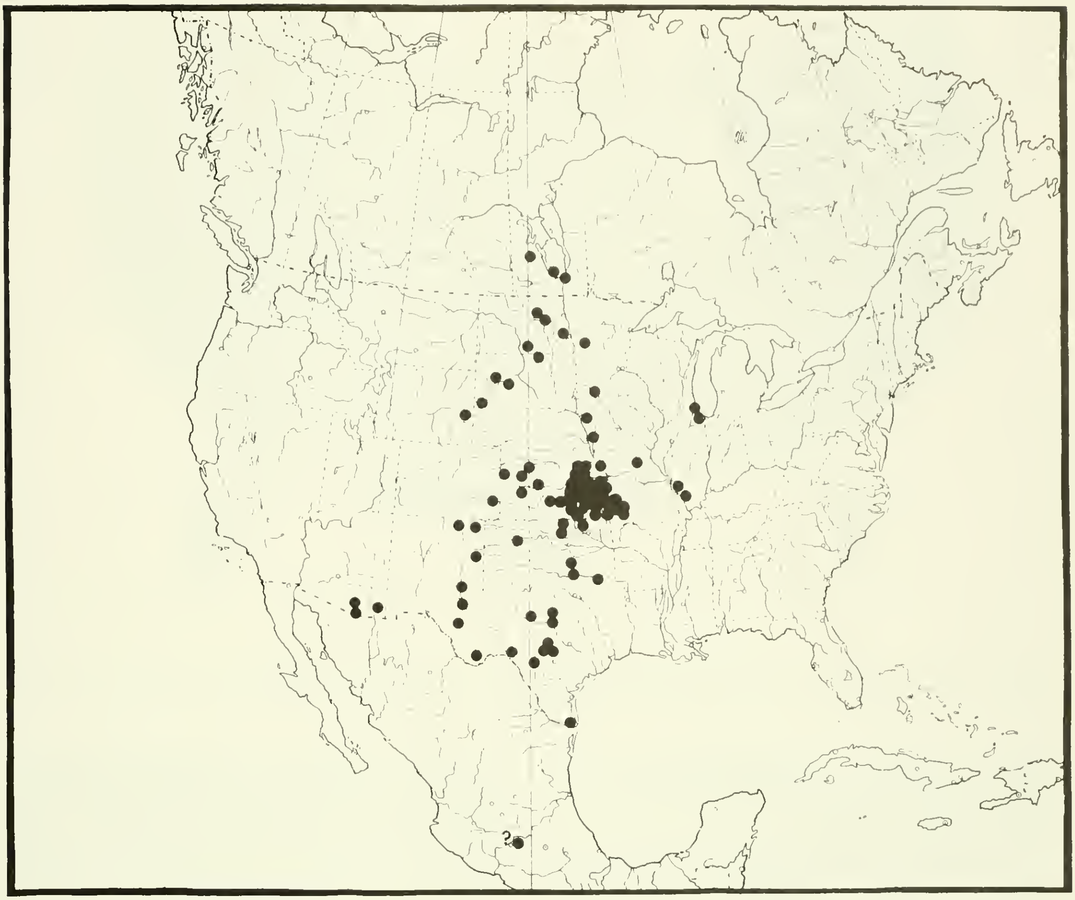

Fig. 46. Geographic distribution of *Flexamia prairiana*.

(tentatively) without dissection. The *prairiana* face type is almost always distinguishable from the faces of *graminea*, *sandersi*, *delongi*, or *dakota*, which may occur with it in *Andropogon* prairies. Dissected male specimens reveal an aedeagus that might be confused only with that of *reflexa*. Female specimens may prove difficult to identify because the bases of the first valvulae vary geographically. In southwestern populations this structure is rarely sclerotized, as illustrated by Young and Beirne (1958).

36. *Flexamia reflexa* (Osborn & Ball)

*Deltocephalus reflexus* Osborn & Ball 1897: 203.
*Deltocephalus (Flexamia) reflexus*, DeLong 1926: 28.
*Flexamius reflexus*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (3.1–4.0) mm, of ♀ 3.7 (3.2–4.2) mm. Crown moderately produced (1.49 x interocular width; 0.68 x head width) (♂ n = 20; ♀ n = 15). Face variable, often pale on lower half with broad interocular band; band may be obscured in dark specimens. [♂] Pygofer (Fig. 62X) with posterior lobe strongly produced, truncate apically. Plates (Fig. 45B) elongate, without notches or lateral projections. Connective in lateral aspect with dorsal keels extending almost as far dorsad as aedeagal apodeme. Aedeagus (Fig. 44D) asymmetrical, shaft elongate, gradually tapered; gonopore anteapical on anterodorsal surface, associated with short, apically grooved, unpaired process. Paired apical processes serrate along ventral edge, extending basad less than half length of shaft in lateral aspect. [♀] Ovipositor

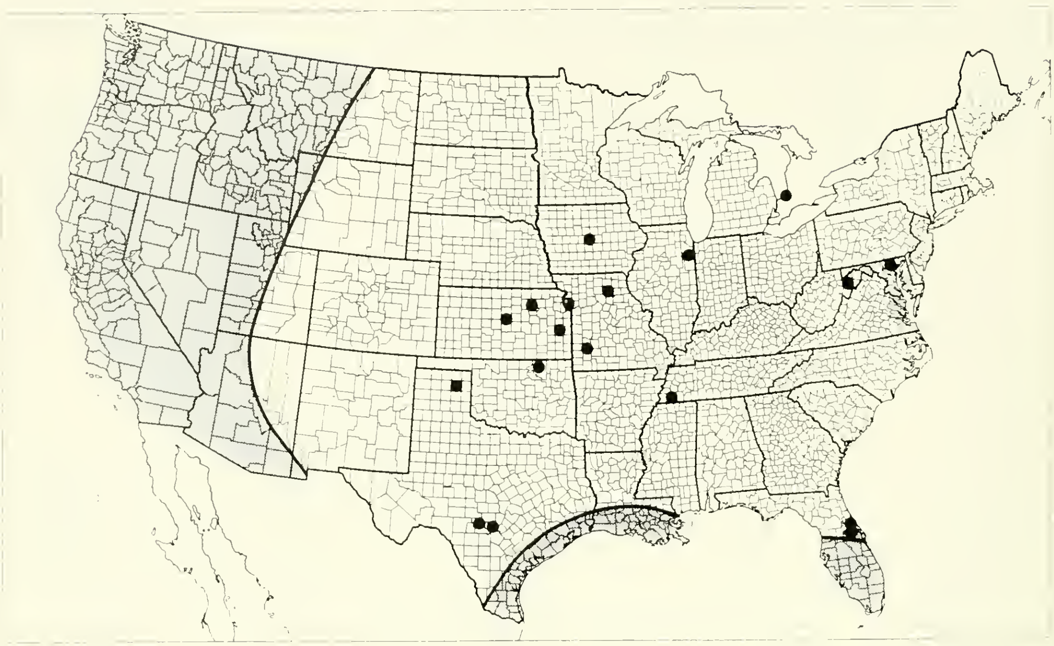

Fig. 47. Geographic distribution of *Flexamia reflexa* and a host, *Andropogon gerardii*.

with first valvulae membranous basally, not curved dorsad; sclerotized portion obliquely truncate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Tall-grass prairie (Cwikla and Blocker 1981), savanna, and glades and prairie mosaic of deciduous forest, Kansas and Iowa to Texas, Ontario, Maryland, and Florida (Fig. 47).

BIOLOGY.—This species is associated with *Andropogon gerardii* in the East (Maryland and West Virginia) and may be associated with that host in the tall-grass prairie. However, in Texas it occurs in mixed-prairie associations in which big bluestem is a minor component.

DIAGNOSIS AND REMARKS.—Given the paucity of specimens of *reflexa* in collections, it is remarkable that it was the second member of the *prairiana* group to be described and that it is the type species of the genus. Almost all uncleared specimens "identified" as this species in museum drawers turn out to be other *prairiana* group species. The abundant *prairiana*, which occurs through much of its range on little bluestem (*Schizachyrium scoparium*), is much more apt to be encountered in the prairie. Since we have found no reliable external characters for sorting *reflexa* from *prairiana*, a search for this species involves sifting through numerous *prairiana* specimens. The position of the gonopore (some distance from the aedeagal apex, situated basally on a short, appressed, unpaired process) contrasts sharply with the simpler, oval, anteapical gonopore of *prairiana*. Some specimens of *atlantica* and *producta* may also resemble *reflexa* in general facies, but their genitalia bear little resemblance to those of *reflexa*.

### 37. *Flexamia atlantica* (DeLong)

*Deltocephalus (Flexamia) atlanticus* DeLong 1926: 29.
*Deltocephalus atlanticus*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.2–4.2) mm, of ♀ 4.1 (3.6–4.5) mm. Crown moderately produced (1.31 x interocular width; 0.59 x head width) (♂ n = 20; ♀ n = 20). Face black in upper half, often forming interocular band contrasting with pale lower half. [♂] Pygofer (Fig. 62Y) with posterior lobe narrow, without ventral lobe. Plates (Fig. 45C) elongate, notched apically. Aedeagus (Fig. 44A) asymmetrical, shaft nearly uniform in width, gonopore simple, anteapical on

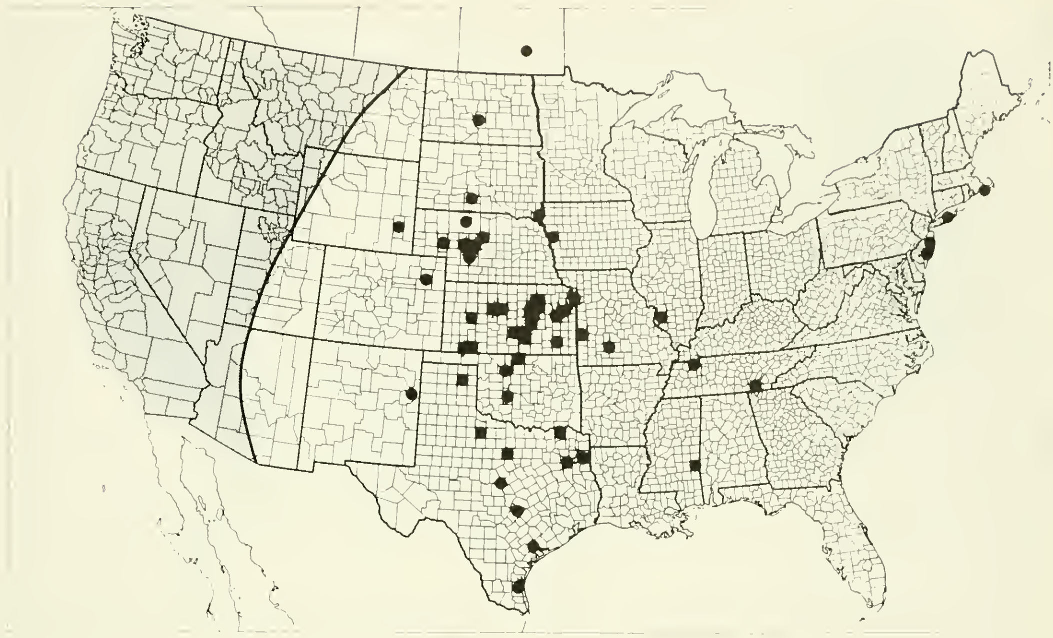

Fig. 48. Geographic distribution of *Flexamia atlantica* and a host, *Panicum virgatum*.

the right side. Pair of elongate, retrorse, serrate, apical processes extending basad approximately half length of shaft. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63DD) not curved dorsad.

GEOGRAPHIC DISTRIBUTION.—Prairie from Manitoba, North Dakota, Wyoming, and New Mexico east to Illinois (Fig. 48). Also along the Atlantic coastal prairie of the Northeast, and very patchily in the Southeast.

BIOLOGY.—In tall-grass prairie *atlantica* is usually associated with switchgrass (*Panicum virgatum*). This grass, a dominant in the northeastern coastal prairie, probably accounts for the occurrence of *atlantica* there. In mixed-prairie and southwestern grasslands, *atlantica* occurs on native *Sporobolus* spp. and is the major *Flexamia* colonist in the extensive stands of two exotic chloridoid grasses (weeping love grass [*Eragrostis curvula*] and bermudagrass [*Cynodon dactylon*]) in Texas and Oklahoma.

OLIGOPHAGY COEFFICIENTS.—Texas and Oklahoma: Gramineae 0.994; Chloridoideae 1.000; *Eragrostis curvula* 0.243; *Cynodon dactylon* 0.633 (n = 161). Kansas, Missouri, and Nebraska: Gramineae 1.000; Panicoideae 0.876; *Panicum virgatum* 0.783; *Sporobolus* spp. 0.124 (n = 177).

DIAGNOSIS AND REMARKS.—*Flexamia atlantica* is the only pale-faced *Flexamia* prairie species with apically notched plates. Also, individuals of *atlantica* tend to be larger than those of *reflexa* or *prairiana*. In the Southeast, *atlantica* may occur with *producta*, which tends to be smaller, and which usually has a much more produced crown. Although these characters permit tentative recognition, definitive recognition is readily accomplished by examining the aedeagal morphology, which is unique.

### 38. *Flexamia producta* (Walker)

*Iassus productus* Walker 1851: 891.
*Deltocephalus visendus* Crumb 1915: 189.
*Deltocephalus (Flexamia) productus*, DeLong 1926: 43.
*Flexamia producta*, DeLong and Knull 1945: 35.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (3.0–3.5) mm, of ♀ 3.5 (3.2–3.9) mm. Crown usually conspicuously produced (1.62 x interocular width; 0.75 x head width) (♂ n = 20; ♀ n = 20). Face variable but usually with clearly delimited interocular band; band occasionally obscured in darker specimens. [♂] Plates

Fig. 49. Geographic distribution of *Flexamia dakota* (●) and *producta* (■) and the host of *dakota*, *Scizachyrium scoparium*, which does not occur on the Atlantic coastal plain.

(Fig. 45D) elongate, notched at apex. Pygofer (Fig. 62AA) with posterior lobe produced and rounded apically, ventral portion extending mesad as pronounced lobe, serrate along margin, the two lobes often overlapping in ventral aspect (but not necessarily in prepared specimens). Aedeagus (Fig. 44E) asymmetrical apically; shaft elongate, slender, slightly swollen anteapically; gonopore irregularly oval, on left side of dorsal surface of shaft; pair of processes arising asymmetrically at apex of shaft, extending basad almost half of shaft length, each process laterally compressed and conspicuously toothed along ventral edge; with short, small, curved process arising near proximal portion of gonopore, extending sinistrad. [♀] Female sternum VII as for group, ovipositor with bases of first valvulae (Fig. 63EE) not curved dorsad, broad basally in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Gulf Coast and Atlantic seaboard from Mississippi to Maryland (Fig. 49).

BIOLOGY.—This species has been collected commonly in coastal prairies, but there are few host records. We have recorded it from several exotic chloridoid grasses (e.g., *Zoysia japonica* and *Cynodon dactylon*) in Maryland but have little field experience in the coastal prairies where it is most abundant. We note that *Sporobolus virginicus* is a common dominant in southeastern coastal prairies; this chloridoid grass should be examined as a possible natural host. On the other hand, there are indications that cicadellid host specialization decreases in mesic and wet prairies (Whitcomb et al. 1987, 1988). Given its occurrence in wet southeastern grasslands, *producta* may turn out to be a habitat specialist.

DIAGNOSIS AND REMARKS.—The produced crown of this species affords a tentative indication of its identity. Unfortunately, *satilla* and *sandersi*, which occur with *producta*, also have produced crowns that approach the length/width ratios of *producta*. Although the latter species are similar to *producta* in most aspects, their faces are without conspicuous interocular bands. It is therefore possible to sort, from an assemblage of southeastern *Flexamia*, a large subset of *producta* specimens that have either an extremely produced crown or a distinct interocular band (or both). Unfortunately, this will leave a mixture of atypical

*producta* specimens and specimens of *sandersi* and *satilla*, or perhaps even *clayi*. The aedeagal characters of *producta* readily diagnose the species.

### 39. *Flexamia dakota* Young & Beirne

*Flexamia dakota* Young & Beirne 1958: 44.

IMPORTANT CHARACTERS.—Length of ♂ 3.0 (2.8–3.6) mm, of ♀ 3.3 (3.0–3.6) mm. Crown moderately produced (1.40 x interocular width; 0.64 x head width) (♂ n = 21; ♀ n = 18). Face brown to tan, with parallel lines. [♂] Pygofer (Fig. 62BB) with upper portion of posterior lobe produced posteriorly. Plates (Fig. 45E) with apical third narrowed. Aedeagus (Fig. 44I) symmetrical; shaft elongate, slender, narrower near midlength than at base or apex. Gonopore anteapical on anterodorsal surface; pair of recurved processes extending basad amost half length of shaft; each process serrate on ventral margin. [♀] Sternum VII as for group. Ovipositor with bases of first valvulae broadest near base (Fig. 63KK).

GEOGRAPHIC DISTRIBUTION.—Semiarid Great Plains of western North and South Dakota, eastern Wyoming, Nebraska Sand Hills to Oklahoma, and the Edwards Plateau of Texas (Fig. 49). A presumably disjunct population occurs in the Loess Hills of western Iowa. This species has recently been recorded from Mexico (2 ♂, 42 km S Piedras Negras, Coahuila, 13 October 1987, A. L. Hicks and J. E. Lowry).

BIOLOGY.—This species is apparently a specialist on little bluestem (*Schizachyrium scoparium*) in dry prairie.

OLIGOPHAGY COEFFICIENT.—Gramineae 1.000; Panicoideae 0.990; *Schizachyrium scoparium* 0.990 (n = 209).

DIAGNOSIS AND REMARKS.—This species often occurs in the absence of other specialists of andropogonoid grasses. However, in the Edwards Plateau of Texas, *dakota* occurs with *graminea* (which it closely resembles in general facies), *prairiana*, and, rarely, *reflexa*. Although it can be tentatively sorted from the latter two species on the basis of face pattern, we have found no reliable external character to sort it from *graminea*. The symmetrical aedeagus of *dakota*, which has only paired apical processes, is unique. Young and Beirne (1958) described only males; Lowry and Blocker (1987) described the female.

### 40. *Flexamia sandersi* (Osborn)

*Deltocephalus sandersi* Osborn 1907: 164.
*Deltocephalus (Flexamia) sandersi*, DeLong 1926: 27.
*Flexamia sandersi*, DeLong and Sleesman 1929: 83.
*Flexamius bidentata* DeLong 1935: 155.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (2.9–3.5) mm, of ♀ 3.4 (3.2–3.9) mm. Crown produced (1.48 x interocular width; 0.69 x head width) (♂ n = 11; ♀ n = 10). Face (Fig. 3H) varying from dark above and shading to paler apically to brown or black throughout, in former case with dark area shading gradually along lower margin; no interocular band. [♂] Pygofer (Fig. 62CC) truncate on dorsal portion of posterior margin. Plates (Fig. 45F) elongate, apically notched, in some specimens bidentate. Aedeagus (Fig. 44B) asymmetrical; shaft elongate, gradually tapered; gonopore on dorsolateral surface of shaft at base of retrorse, unpaired process, which is closely appressed to the shaft, has one minutely serrate margin, and extends basad to midlength of shaft; pair of apical, retrorse processes, dorsal slightly longer than ventral, each acute apically and with distinctly serrate margin. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63FF) not curved dorsad.

GEOGRAPHIC DISTRIBUTION.—Eastern Kansas to Louisiana, east to southern Illinois, Massachusetts, and South Carolina (Fig. 50).

BIOLOGY.—The principal host appears to be broomsedge (*Andropogon virginicus*), but this conclusion requires further study.

DIAGNOSIS AND REMARKS.—Throughout much of its range, *sandersi* occurs with *clayi*. These species usually have been collected in the summer before their host grasses have flowered. Many host records are listed simply as "*Andropogon* sp." In the Maryland Piedmont *sandersi* occurs abundantly on broomsedge in the absence of *clayi;* in Maryland we have found the latter species only in the Appalachians. We have found no reliable external character that separates *sandersi* from *clayi*, *satilla*, *graminea*, or *delongi*. However, the characters of the aedeagus described above and in the key readily separate *sandersi* from all other *prairiana* group species, with the exception of *delongi*. We have discussed the relationship of these very closely related sister species in the corresponding section under *delongi*.

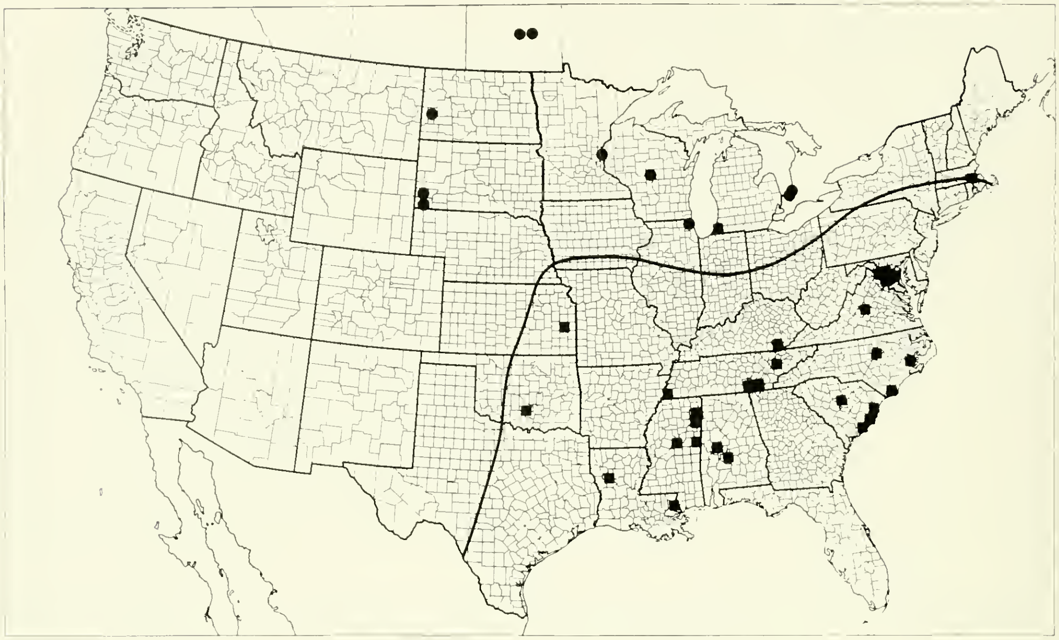

Fig. 50. Geographic distribution of *Flexamia sandersi* (■) and *delongi* (●) and the presumed major host of *sandersi*, *Andropogon virginicus*.

## 41. *Flexamia delongi* Ross & Cooley

*Flexamia delongi* Ross & Cooley 1969: 246.
*Flexamia sandersi*, Young and Beirne 1958: 164. (In part.)

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.4–4.1) mm, of ♀ 3.8 (3.4–4.4) mm. Crown variably produced (1.34 x interocular width; 0.65 x head width) (♂ n = 17; ♀ n = 21). Face varying from dark above, shading to paler apically to black or brown throughout, dark area often fading gradually along lower margin, interocular band absent. [♂] Pygofer and plates as in *sandersi*. Aedeagus (Fig. 44C) asymmetrical; shaft elongate, not cylindrical, gradually tapered; gonopore on dorsolateral surface at base of retrorse process, which extends basad to midlength of shaft; pair of lateral, apical, retrorse processes extending more than one-third but less than one-half length of shaft, each with a distinct, coarsely serrate margin and with very acute apex. [♀] Sternum VII as for group; ovipositor with base of each first valvula as for *sandersi*.

GEOGRAPHIC DISTRIBUTION.—Northern Indiana and Illinois, Wisconsin, and Ontario, west to South Dakota, Saskatchewan, and Manitoba (Fig. 50).

BIOLOGY.—This species is presumably a specialist of little bluestem, *Schizachyrium scoparium*.

DIAGNOSIS AND REMARKS.—The pair of sister species consisting of *delongi* and *sandersi* is (with the exception of *satilla* and *clayi*) the most closely related of all *Flexamia* sister pairs. Ross and Cooley (1969) acknowledged this closeness, pointing out that *delongi* previously had been considered a variant of *sandersi*. Ross and Cooley examined material from the East but did not examine specimens from Canada or from the Dakotas. Thus, their interpretation of *delongi* as a geographic replacement for *sandersi* made the identity of the northern prairie material a crucial test. We examined specimens from these regions from the USNM and CNC and found them to be referable to *delongi*. We retain herein the concept of *delongi*, because it can be defended on morphological, biological, and historical grounds. The species occurs in a region that was largely or completely glaciated during the Wisconsinan. The principal (or sole) host of *sandersi* (*Andropogon virginicus*) does not occur in this region. Thus, *sandersi* and *delongi* appear to utilize different

hosts, whose phenological asynchrony may reinforce reproductive isolation. Finally, although genitalic differences between *delongi* and *sandersi* are slight, they are consistent. The apical, aedeagal processes of *delongi* are more divergent than those of *sandersi;* each process has 6–9 teeth. Further, the gonopore extension is more divergent from the shaft than in *sandersi.*

In the northern prairies *delongi* may occur on little bluestem with *graminea*, *prairiana*, or *dakota*, but its aedeagal structure readily separates it from these species.

### 42. *Flexamia graminea* (DeLong)

*Deltocephalus (Flexamia) gramineus* DeLong 1926: 30.
*Flexamius gramineus*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.6 (3.3–4.0) mm., of ♀ 3.7 (3.4–4.1) mm. Crown moderately produced (1.40 x interocular width; 0.68 x head width) (♂ n = 25; ♀ n = 20). Face variable, from entirely stramineous to stramineous with clypeus darkened, from tan to almost black with pale arcs; interocular band absent. [♂] Pygofer (Fig. 62EE) with posterior lobe not well differentiated ventrally, posterodorsal portion produced caudodorsad and truncate apically. Plates (Fig. 45H) divergent at apex, often appearing to be notched. Aedeagus (Fig. 44F) asymmetrical; shaft elongate, slender, twisted in apical half; gonopore consisting of a spiral groove originating at shaft midlength; pair of asymmetrical, retrorse, apical processes, with one minutely serrate edge. [♀] Sternum VII as for group. Ovipositor with base of each first valvula (Fig. 63LL) angular in dorsal aspect, narrowly curved dorsad anterolaterally, recurved portion extending only slightly dorsad.

GEOGRAPHICAL DISTRIBUTION.—Tall-grass prairie of North Dakota, Kansas to Blackland Prairie, and south Texas east to Missouri and Illinois (Fig. 51). A specimen from the Ball collection is labeled "DC." If this is an abbreviation for "District of Columbia," and if the hastily scrawled, penciled label is correct, then it would be necessary to explain a widely disjunct distribution for *graminea*. Recently, little bluestem and several unusual prairie forb species have been found in a band of savannalike habitat along the north bank of the Potomac River between Great Falls Park (Maryland) and the District of Columbia (D. Boone, personal communication). The possibility that *graminea* (and perhaps other prairie insects) may have colonized such a habitat cannot be completely discounted.

BIOLOGY.—This species appears to be a specialist of little bluestem (*Schizachyrium scoparium*), but in late summer it may take refuge on other hosts.

OLIGOPHAGY COEFFICIENT.—*Schizachyrium scoparium* 0.91.

REMARKS AND DIAGNOSIS.—Throughout most of the tall-grass prairie, *graminea* occurs regularly with *prairiana* on little bluestem. It can be distinguished from *prairiana* by its consistent lack of an interocular band and by its notched plates. However, through portions of its range it may also occur with *sandersi*, *dakota*, or *delongi*, or in mixed-prairie habitats with *atlantica* or *reflexa*. The structure of its aedeagus separates it readily from these species, but it is most closely related to *clayi* and *satilla*. For differential diagnosis of these three species, see the corresponding section under *clayi*.

### 43. *Flexamia clayi* Young & Beirne

*Flexamia clayi*, Young and Beirne 1958: 64.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.3–4.0) mm, of ♀ 3.7 (3.1–3.8) mm. Crown variably produced (1.44 x interocular width; 0.71 x head width) (♂ n = 20; ♀ n = 20). Face brown to black above, usually shading gradually to paler below. [♂] Pygofer (Fig. 62DD) with posterior lobe more distinct than in *graminea*. Plates (Fig. 45I) divergent apically, outer margins widened at midlength. Aedeagus (Fig. 44H) much as in *graminea* but with shaft usually much more expanded at base of gonopore. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63GG) rounded, with recurved portion broader than in *graminea*.

GEOGRAPHIC DISTRIBUTION.—Appalachian region from Maine to north Georgia, west to Illinois (Fig. 51).

BIOLOGY.—Some records for *clayi* are for broomsedge (*Andropogon virginicus*); others are for little bluestem (*Schizachyrium scoparium*). Many are for "*Andropogon*." Since broomsedge does not occur in Maine, at least some of the records for little bluestem must be correct. Many records, including our own, are

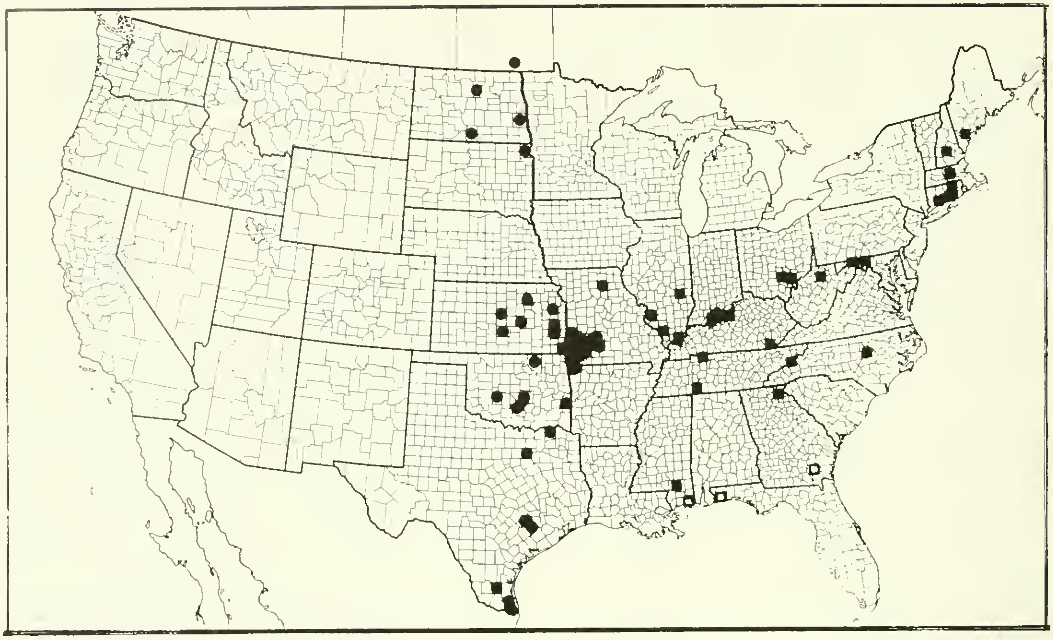

Fig. 51. Geographic distribution of *Flexamia graminea* (●), *clayi* (■), and *satilla* (□).

inadequate to discriminate between these two andropogonoid grasses.

REMARKS AND DIAGNOSIS.—We are unaware of any region in which *graminea*, *clayi*, or *satilla* occur together. As in the case of *sandersi* and *delongi*, they may represent vicariant populations that have become reproductively isolated and diverged morphologically. The initial description of *clayi* from Kentucky, and subsequent collections of the species from Georgia and Tennessee, obscured the extent of the range of *clayi*. Our collections of the species from Ohio and the Maryland and West Virginia Alleghenies, and identification of material from Maine and New Hampshire as *clayi* present a different picture, portraying the species as a cool-temperate species of the eastern mountains. This contrasts with that of *graminea*, whose range is essentially the tall-grass prairie, and *satilla*, whose known range is the Gulf Coast (Florida and south Georgia to Mississippi).

Members of this complex can be readily separated from other *prairiana* group species by aedeagal characters. The aedeagal shaft of *clayi* is much more expanded basad of the gonopore than the usual condition in *graminea*. However, some specimens of *graminea* from south Texas have a basally expanded gonopore that could be confused with that of *clayi*. The most consistent character that separates *clayi* and *graminea* is the condition of the anteapical lobes of the apodemal processes. In *clayi* the processes each have a prominent anteapical lobe, which is directed mesad. The shaft in *satilla* is much narrower than that of *clayi*.

## 44. *Flexamia satilla* Hamilton & Ross

*Flexamia satilla* Hamilton & Ross 1975: 606.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.3–3.4) mm, of ♀ 3.6 mm. Crown produced (1.49 x interocular width; 0.74 x head width). Face variable, but without distinct interocular band; usually dark brown or nearly entirely black. [♂] Genitalia much as in *clayi*, but with aedeagal shaft ( Fig. 44J) not as expanded at base of gonopore. [♀] Sternum VII as for group; ovipositor with base of first valvula rounded, with recurved portion broad and extending dorsad.

GEOGRAPHICAL DISTRIBUTION.—The type locality in south Georgia is just north of

Okefenokee Swamp. We have found other specimens, collected by Beamer, from the Gulf Coast in Florida and Mississippi.

BIOLOGY.—This species was collected on an andropogonoid grass, probably *Andropogon virginicus* (K. G. A. Hamilton, personal communication).

REMARKS AND DIAGNOSIS.—This species is sympatric with *producta* in the Gulf Coast region, and two specimens had been filed in the KU collection in the *producta* drawer. These specimens were tentatively separated from *producta* by the face, which was black, without a conspicuous interocular band. Unfortunately, some specimens with equally dark faces turned out, when they were cleared, to be *producta*. It is therefore easy to understand how this species escaped recognition for many years.

The degree of genitalic difference between *clayi* and *satilla* falls well within that considered by some workers to represent geographic variation. However, we feel that *satilla* is subject to the same phenological constraints as *producta*. The hypothesis that the *graminea* complex in the East is divided into Appalachian and Gulf Coast species seems reasonable, and, given our ability to distinguish the species on (admittedly minor) morphological grounds, justifies retention of *satilla*.

This species is safely separated from its sympatric cohort, *producta*, only by genitalic examination, although the latter species (unlike *satilla*) often has a distinct interocular band. For distinctions within the *clayi* complex, see the comparable section under *clayi*.

## BIOLOGY OF *FLEXAMIA*

*Flexamia* species are residents of North American grasslands, where they specialize predominantly on dominant, warm-season grasses (Panicoideae and, especially, Chloridoideae). Several species, however, appear to breed on sedges (Cyperaceae) or rushes (Juncaceae). The genus is divided into 13 species groups; host choice is related to membership in these groups.

No *Flexamia* species are known to be univoltine; as a result, they are inhabitants of mesic grasslands and are poorly adapted for semiarid grasslands. The habitats of the genus include true prairie, short-grass plains, semitropical grasslands, high desert plains or montane grasslands, riparian grasslands, and saline or nonsaline lakeshores.

In semiarid grasslands, grass hosts that support *Flexamia* species tend to be capable of growth with minimal precipitation, but are unlikely to undergo repeated episodes of dormancy through the summer. Perhaps this is why, despite their proclivity for chloridoid grasses, not a single *Flexamia* species specializes on *Hilaria* or *Sporobolus* species. This is true despite the fact that some members of these grass genera are among the major dominants in southwestern grasslands and comprise a significant fraction of the regional grassland biomass. [Note: As a control to this "natural experiment," *Hilaria* and *Sporobolus* species have acquired specific non-*Flexamia* cicadellid guilds of their own (Whitcomb et al. 1987).]

The relation of *Flexamia* species to their hosts ranges from habitat specialization (in primitive species), to various degrees of inter- and intrageneric oligophagy, to absolute monophagy. Narrow oligophagy is the most common strategy. Body size of *Flexamia* species appears to be correlated with size of the host plant. Intraspecific variation in body size may reflect host plant quality; individuals from populations at the range periphery are often small.

*Flexamia* species respond to several aspects of grassland structure. Disturbances such as mowing or burning tend to reduce populations or to extirpate them altogether; for this reason *Flexamia* is an excellent genus for assessing habitat quality of grassland reserves (Whitcomb 1987). On a local level, populations of *Flexamia* species are almost always much higher in more mesic segregates of grasslands defined by minor topographic variation than in adjacent xeric sites (Whitcomb et al. 1987). On a regional level the degree of fidelity to single hosts appears to be least in mesic prairie or, perhaps, in southeastern grasslands (Whitcomb et al. 1987). The structure of grassland dominance hierarchies may determine host choice.

Habitat patchiness has had a profound effect on *Flexamia* species on both historical and contemporary time scales. For monophagous species, their hosts are evolutionary islands. Contemporary host patchiness may affect

presence or absence of *Flexamia* species within their ranges. However, no *Flexamia* species is able to track its host throughout the entire range of the host. This not only is the result of patchy host occurrence at the range periphery, but is often reinforced by climate. In many instances host colonization appears to be blocked by climatic factors. For example, the *Flexamia* complex that colonizes side-oats grama (*Bouteloua curtipendula*) is divided into six species, none of which is known to overlap in range. The isolating mechanisms are those associated with the different climatic regimes of prairie, Chihuahuan and Sonoran desert, interdesert grasslands of the Gila Mountains of southeastern New Mexico, and the eastern and western Mexican grasslands. *Buchloë dactyloides*, *Schizachyrium scoparium*, and *Muhlenbergia porteri* are similarly partioned, as is *Bouteloua gracilis* (although less spectacularly so). The possible role of host biotype (in its inherent genetic composition), apart from the purely phenologically determined availability of growing host, has not been determined.

We have seen no evidence that *Flexamia* species are highly fecund; they are rarely captured at lights or in aerial traps. There is no evidence of seasonal movement under conditions that permit observation of immigration of *Athysanella* macropters or *Laevicephalus* adults into suitable grassland. We therefore predict that the life history strategy of *Flexamia* species will be found to resemble K- rather than r-selection (MacArthur and Wilson 1967).

Eggs of most species are presumably oviposited in host tissue. In temperate regions it is reasonable to assume that eggs laid in the field in autumn are in diapause. In central latitudes first-generation adults appear in early June. In subtropical latitudes, such as south Florida and south Texas, collection records from December, January, and February indicate that reproduction may occur throughout the year.

## SPECIES CONCEPT IN *FLEXAMIA*

The species concept that emerges from our treatment of *Flexamia* is a composite of individual decisions concerning species. We faced difficult decisions in several *Flexamia* species groups.

In the *prairiana* group there are three sets of close sisters. In one of these sets (*prairiana-reflexa*), the types differ so substantially that no immediate problem is evident. When specimens from different geographic regions were examined, however, problems emerged. The holotype of *prairiana*, from Illinois, represents the northeastern periphery of the range of this species (Fig. 46). Females from the southwestern part of the range, especially those from the montane grasslands of the Chihuahuan Desert region or the Trans-Pecos shrub savanna, differ from northern individuals in certain features of the first valvulae; these populations colonize *Bothriochloa* spp. rather than little bluestem (*Schizachyrium scoparium*). However, we found no characters of the male genitalia that distinguish the *Bothriochloa* populations. Further, as discussed by Young and Beirne (1958), the male aedeagal characteristics of *reflexa* and *prairiana* vary intraspecifically. It appears that both species, although widespread, are distributed patchily in some parts of their ranges. Under these circumstances it is reasonable to suspect the existence of reproductively isolated populations. For example, we would not be surprised if the Chihuahuan populations of *prairiana* proved to be reproductively isolated from the tall-grass prairie populations.

Our decision to retain species concepts proposed by Ross and Cooley (1969) and Hamilton and Ross (1975) defining the *sandersi-delongi* and *satilla-clayi* sister pairs has been discussed under the species descriptions of *delongi* and *satilla*. In each case we elected to retain the newly described species on the criterion of probable phenological isolation and consistency of (admittedly) minor morphological differences.

The Anasazi form of *arenicola* presents a more difficult problem. This population, centered in the Four Corners area of the Southwest, is reproductively isolated from populations of *arenicola* in the Nebraska Sand Hills. Further, it has a distinctive morphological characteristic—the unpaired, aedeagal process is invariably broken, presumably in copulation. Although this character tends to define the Anasazi form, we have found one specimen of *arenicola* from Nebraska with a broken aedeagus. Thus, despite our strong suspicion

that a certain amount of morphological divergence has occurred between the two populations, we have found no consistent character to separate the two populations. Because we feel that a taxonomic designation is inappropriate, we refer to the Four Corners population simply as the Anasazi form of *arenicola*.

The *celata-stylata* and *beameri-texana* sister pairs also merit brief mention. The distinctive process of the male pygofer that occurs in both members of the *celata-stylata* set suggests that the divergence is relatively recent. Because the area of present-day occurrence of *celata* was largely created by the most recent glacial maximum (Wright 1970), we at first thought that this speciation event was Holocene in origin, as the minor degree of morphologic divergence would suggest. The geographic proximity of the ranges of the two species seemed to suggest that speciation occurred by dispersal of *stylata* or a similar ancestor into sandhill grasslands that emerged postglaciation. However, the morphological evidence contradicts this tidy explanation. The aedeagal symmetry of *celata* and the presence of presumably plesiomorphic, tapered, notched plates similar to those of *arenicola* or *decora* demand that *celata* be considered the most closely related to the ancestral lineage. Perhaps during various glacial episodes sandy grasslands were much more common than they are today. The existence of three other uncommon sand-inhabiting *Flexamia* species (*grammica*, *arenicola*, and *areolata*), in combination with other studies (Whitcomb et al. 1986, 1987, 1988) indicating that only dominant grasses accumulate specialists, supports this hypothesis.

The divergence of *texana* and *beameri* is also unclear. This murkiness is perhaps an artifact of the rarity of the species; each is known from single collections of E. D. Ball and R. H. Beamer, respectively. We therefore know little of the ecology of these species. Each of these species occurs just outside the periphery of the known range of *inflata*, in one case in a cold region in New York, in the other a hot region of south central Texas. The propensity of *inflata* to form ephemeral, isolated colonies on a variety of hosts (Whitcomb et al. 1986) ought, theoretically, to spawn peripheral new species. Although *beameri* and *texana* appear to be closely related, the biogeographic data suggest that an independent origin for the two species from the *inflata* lineage should not be completely discounted.

Species problems in the *prairiana* and *flexulosa* groups, though interesting and challenging, pale when compared to the *pectinata* group. This group, prior to this study, consisted of only two species. We now report expansion of the group to nine species. Three of the new species (*mescalero*, *jacala*, and *collorum*) differ profoundly from previously recognized species. The remaining four species (*gila*, *bandarita*, *minima*, and *zamora*) are closely related members of a complex that includes the previously recognized *pectinata* and *doeringae*. It is likely that all of the species are specialists of side-oats grama (*Bouteloua curtipendula*). This grass host is important (in many regions dominant) throughout most of the prairie, from North Dakota to Ohio to Kansas to north Texas to eastern New Mexico; throughout this region of importance the characters of the styles, aedeagal tips, and female sternum VII of *pectinata* are relatively constant. Similarly, populations of *doeringae* in southeastern Arizona (where the climate has a strong Sonoran influence) show an intraspecifically constant profile in the morphology of the aedeagus, style, and female sternum VII. We now report discovery of a species (*bandarita*) from the Chisos Mountains and Marathon Basin of Texas which, in some respects, is intermediate between *pectinata* and *doeringae*. *Flexamia bandarita* occurs in an area that is rich in endemism, as attested by our description herein of *zacate*, a new Chihuahuan sister of the Sonoran *canyonensis*.

We were delighted to find this endemic until we examined *Flexamia* specimens taken from side-oats grama in the intervening region between the Chisos Mountains and southeastern Arizona that could be referred to neither *bandarita* nor *doeringae*. Rather, they possessed a mosaic of characteristics representative not only of *bandarita* and *doeringae*, but of *pectinata* as well. With collections from three widely separated localities in New Mexico and Chihuahua, Mexico, totaling eleven individuals, we were compelled to recognize another new species (*gila*).

Although we are uncomfortable separating a large complex occurring on a single host into a number of species, we would be even more uncomfortable illustrating the variation

within a single hypothetical polymorphic "species" and attempting to explain why we included such divergent characters under a single name. In our view such a treatment would require redefinition of the species concept in deltocephaline leafhoppers.

Once we recognized the existence of a species complex of side-oats grama specialists, it was easier for us to accept the results of our reexamination of *minima* DeLong & Hershberger and *zamora* DeLong & Hershberger from Mexico. In these examinations we were assisted by the availability of eight previously unidentified specimens referable to *minima* from Monterrey, Mexico, a location considerably north of the type locality. These specimens and the type of *minima* reveal a morphologic profile similar in some respects to *zamora* and *pectinata*, but with substantial differences in the male plates and styles and the female sternum VII. Similarly, on the basis of the female sternum VII and, to a lesser extent, the male plates and styles, *zamora* can be separated from all other members of the complex.

Construction of a map (Fig. 15) of the geographical distribution of members of the complex clarifies the taxonomic status of the species. The distribution of the complex, like that of the host (side-oats grama), encompasses a large percentage of North American grassland area. However, the six species of the complex occur in very different vegetational regions, some of which are recognizable at the biome level. Furthermore, side-oats grama is rare in the Texas mesquite-acacia savanna, so there is an essential discontinuity in host distribution that probably inhibits gene flow between the United States and Mexican populations of side-oats grama specialists. Part of the barrier between *pectinata* and *minima* and *zamora* is, in fact, the area occupied by *doeringae*, *bandarita*, and *gila*. Therefore, the existence of reproductively isolated populations of *Flexamia* specialists on side-oats grama in grasslands of the United States and Mexico is probable, and the reinstatement of *minima* and *zamora* is justified.

The concept of climatically limited specialists that geographically partition a single grass host is supported to some extent by studies in Mexico (Triplehorn and Nault 1985) of *Dalbulus* species, most of which appear to be *Tripsacum* specialists. Further support is given by the recent demonstration (Hicks et al. 1988) that in New Mexico blue grama (*Bouteloua gracilis*) is colonized by seven *Athysanella* species, but that the distribution of each species is confined to regions that are readily interpretable in terms of recognized biogeographic regions (e.g., Colorado Plateau, high plains, short-grass prairie, Chihuahuan grasslands). We believe that *Bouteloua curtipendula* is also partitioned by its *Flexamia* specialists.

In an ideal world we would have postponed all decisions concerning this complex and instead organized an expedition to the Southwest and Mexico to collect *Flexamia* from side-oats grama. However, publication of the conclusions herein need not discourage such exploration; perhaps it will encourage it.

In summary, we have defined *Flexamia* species as populations with consistent and readily demonstrable morphological differences whose reproductive isolation from possibly conspecific populations can be inferred on biogeographic grounds.

## PHYLOGENY OF *FLEXAMIA*

Young and Beirne (1958) established the groundwork for a *Flexamia* phylogeny by their careful descriptions of genitalic and other characters of the genus. Also, although they did not propose a formal phylogeny, they discussed species relationships at some length. With a minimum of assumptions, these proposals and relationships can be presented as a cladogram (Fig. 52).

H. H. Ross was intrigued by *Flexamia* and in 1970 published a preliminary phylogeny of the genus in which the species were identified only by number and no apomorphies were described. Although Ross did not present an explicit proposal, his unpublished notes, which specify apomorphies and synapomorphies, make it possible to diagram his phylogeny also (Fig. 53).

OUTGROUPS.—Ross considered *Spartopyge* Young & Beirne and *Aflexia* Oman to represent *Flexamia* outgroups. Young and Beirne (1958) felt that *Aflexia* was not especially closely related to *Flexamia*. Although the habitus of *Alapus* DeLong and Sleesman is very different (Beamer and Tuthill 1934) from that of *Spartopyge* (Fig. 54), its genitalic characters (Figs. 55F, G) suggest relationship with this genus.

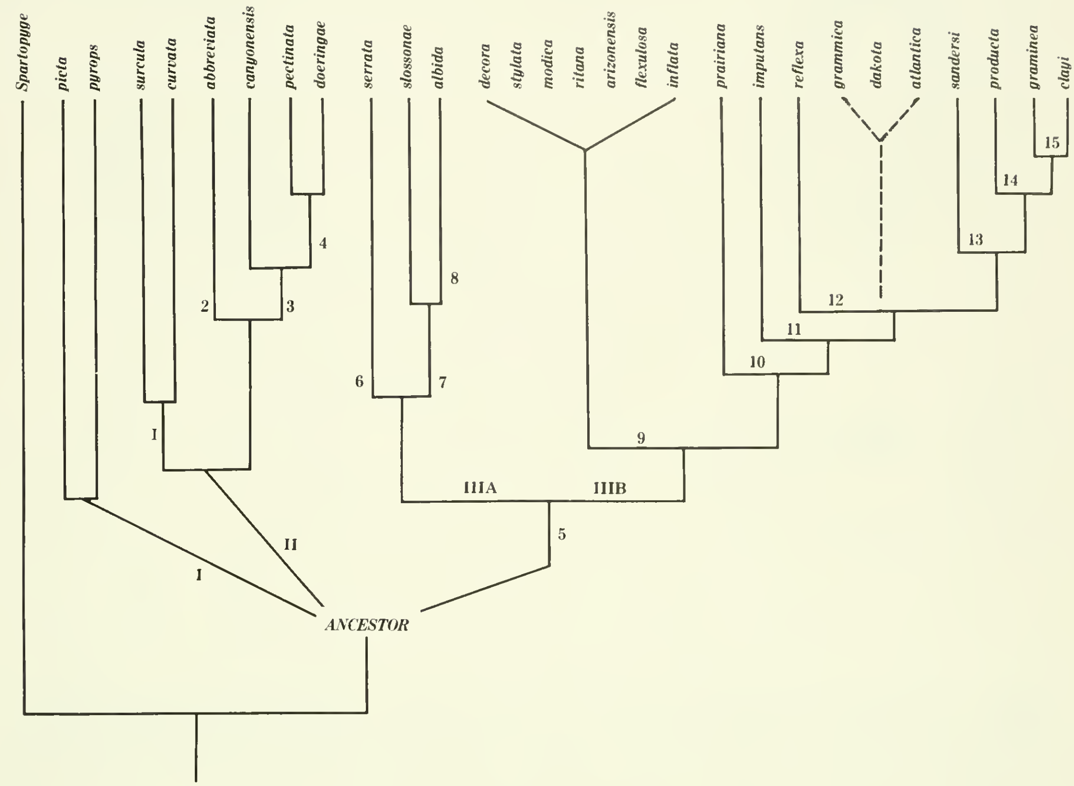


Fig. 52. Species relationships in *Flexamia*: proposal of Young and Beirne (1958). These authors proposed an ancestral condition in which the *Flexamia* aedeagus possessed two pairs of recurved, bilaterally symmetrical appendages at or near the apex of the aedeagal shaft. From this ancestral condition, the authors proposed three or four independent lines of development, without specifying a phylogenetic sequence in which the lines diverged. In one line of development (I), the apical pair of processes tended to fuse and the anteapical to remain separate (*picta* and *pyrops*). In a second line of development (II), the pairs of processes are (1) either preserved, as in *surcula* and *curvata*, or (2) the apical processes are reduced and the basal processes absent (*abbreviata*), or both processes are absent (3) but the location of the gonopore (in *canyonensis*) suggests a derivation from the condition in *abbreviata*. Young and Beirne suggested that *pectinata* and *doeringae*, lacking any trace of aedeagal processes, represent the culmination of one of the developmental lines. We take the liberty of placing these two species (4) at the culmination of line II. In the final lineage the important event was (5) the development of an unpaired ventral aedeagal process. In IIIA this occurred either (6) with additional processes, as in *serrata*, or (7) with branching of more apical processes, as in *slossonae* and *albida*. In *albida* (8) the unpaired ventral process is adherent to the shaft. The final sublineage (IIIB) encompasses most species of the genus. In the more generalized species, the gonopore is small, not elongated, and located on the caudoventral surface of the aedeagus near the apex (9). Young and Beirne placed seven species (*decora*, *stylata*, *modica*, *ritana*, *arizonensis*, *flexulosa*, and *inflata*) in this cluster. In *prairiana* a phyletic torsion of the shaft has occurred (10) so that the gonopore is anteapical on the anterodorsal surface of the shaft. This species has a pronounced groove on the unpaired process, which in *imputans* constitutes the gonopore (11). In *reflexa* the unpaired process is fused basally to the aedeagal shaft (12) but is free at its extremity; the gonopore is circular, but at some distance from the base of the process. In *sandersi* the gonopore has become elongate (13). In *producta* the movement of the gonopore, to the left side of the dorsal surface of the shaft, far removed from the apex, approaches a maximum (14). In *graminea* and *clayi* the unpaired process has almost completely disappeared and the gonopore is spiral (15). In *grammica*, *dakota*, and *atlantica* the anteapical processes have been lost; these species were tentatively placed in line IIIB.

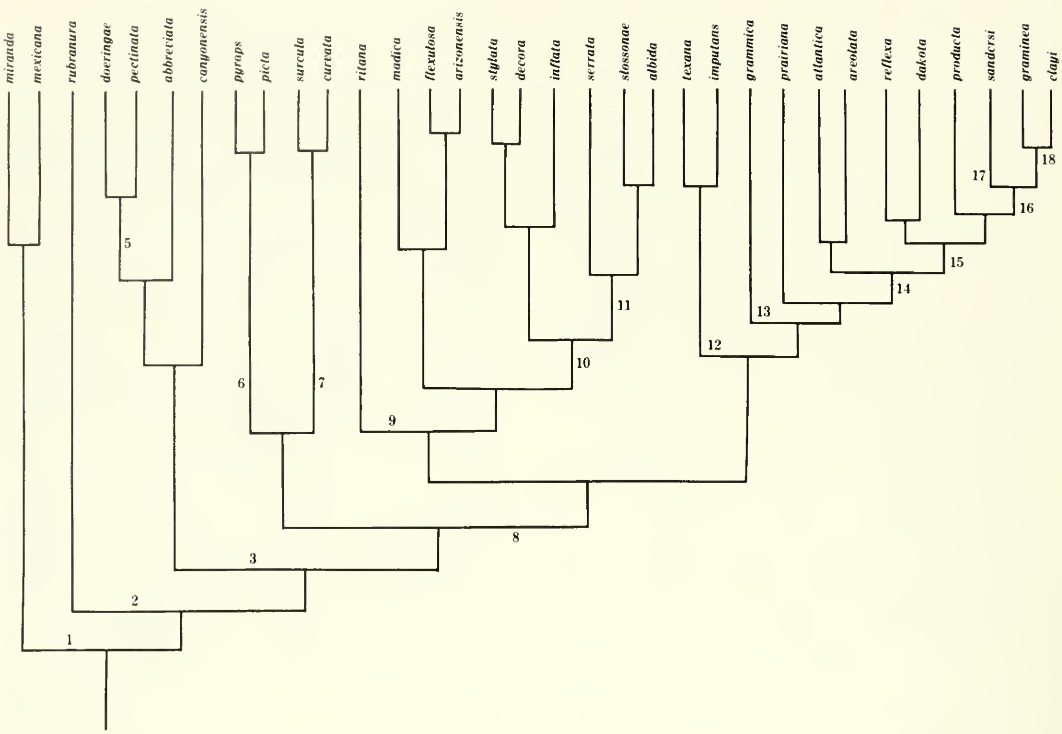


Fig. 53. *Flexamia* phylogeny proposed by Ross (1970, and unpublished notes). The tree diagram was transposed to a cladogram. Identification of species and apomorphies used by Ross to construct the cladogram are taken from unpublished notes. The apomorphies and conserved plesiomorphies designated were (1) mesal brush on pygofer; (2) thin aedeagal shaft with basal processes; (3) lack of aedeagal processes; (4) width of aedeagus, thick (4) or thin (4′); (5) length of male style; (6) angulate pygofer; (7) four aedeagal processes; (8) aedeagus with mesal process; (9) acute aedeagal apex; (10) long, mesal aedeagal process; (11) unpaired aedeagal process bifurcate; (12) aedeagal processes twisted; (13) dorsal location of gonopore; (14) fusion of connective and aedeagus; basal location of median process and gonopore (somewhat = 15, more so = 16); widening (17) of median process to bean-shaped structure appressed to shaft; (18) loss of medial process.

Future phylogenetic hypotheses concerning *Flexamia* should be broadened to include a much wider range of outgroups than those discussed above. Candidates for study should perhaps include *Enantiocephalus* Haupt, a Eurasian genus (Figs. 55A,B). K. G. A. Hamilton (personal communication) has suggested that *Mocuellus* Ribaut and related genera should not be overlooked as outgroups. Finally, we will soon add a new genus (in preparation), presumably also related to *Flexamia*. This genus consists, so far as known, of a single species that specializes on *Muhlenbergia arenacea* in saline flats in semiarid regions of New Mexico and Arizona. The former genus *Acurhinus* (= *Dorydium*) may be more distant from *Flexamia* than once thought (Linnavuori 1959). *Acurhinus maculatus* (Osborn), known only from three females in the Ohio State University collection, is currently regarded as a species of *Hododoecus* Jacoli, an essentially African genus of the Stirellini (Linnavuori and DeLong 1978). It is evident that a phylogeny of deltocephaline genera, especially those with linear connectives articulated with the aedeagus, would greatly enhance all phylogenies of deltocephaline species.

In this study we have chosen two *Spartopyge* species [*miranda* (Knull) and *mexicana* (DeLong & Hershberger)] and *Alapus elongatus* Beamer & Tuthill for outgroup comparison.

PHYLOGENY OF *FLEXAMIA* GROUPS. — We have developed an intuitive phylogeny utilizing many of the characters and concepts

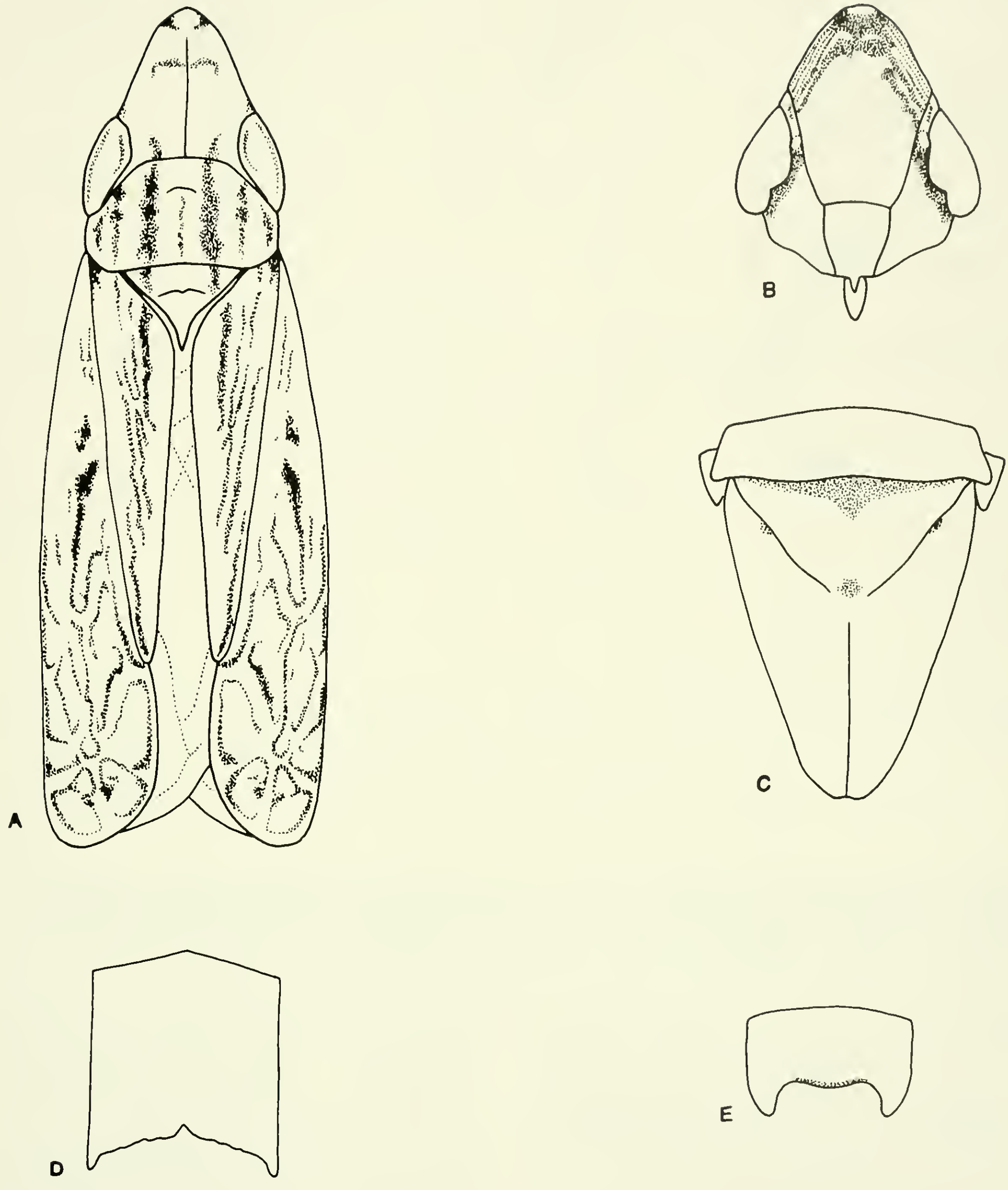


Fig. 54. *Spartopyge* Young & Beirne, the principal *Flexamia* outgroup. *Spartopyge mexicana* (DeLong & Hershberger): A, habitus; B, face; C, male plates, ventral aspect; D, female sternum VII; E, *S. miranda* (Knull), female sternum VII.

developed by Young and Beirne (1958) and Ross (1970, unpublished notes). Details of our reconstruction follow:

*A. Designation of sister species.* We first identified synapomorphies that define close sister species sets. We also assigned polarities within these sets by defining significant autapomorphies of one of the set members.

The sets and defining synapomorphies [s] and autapomorphies [au] were:

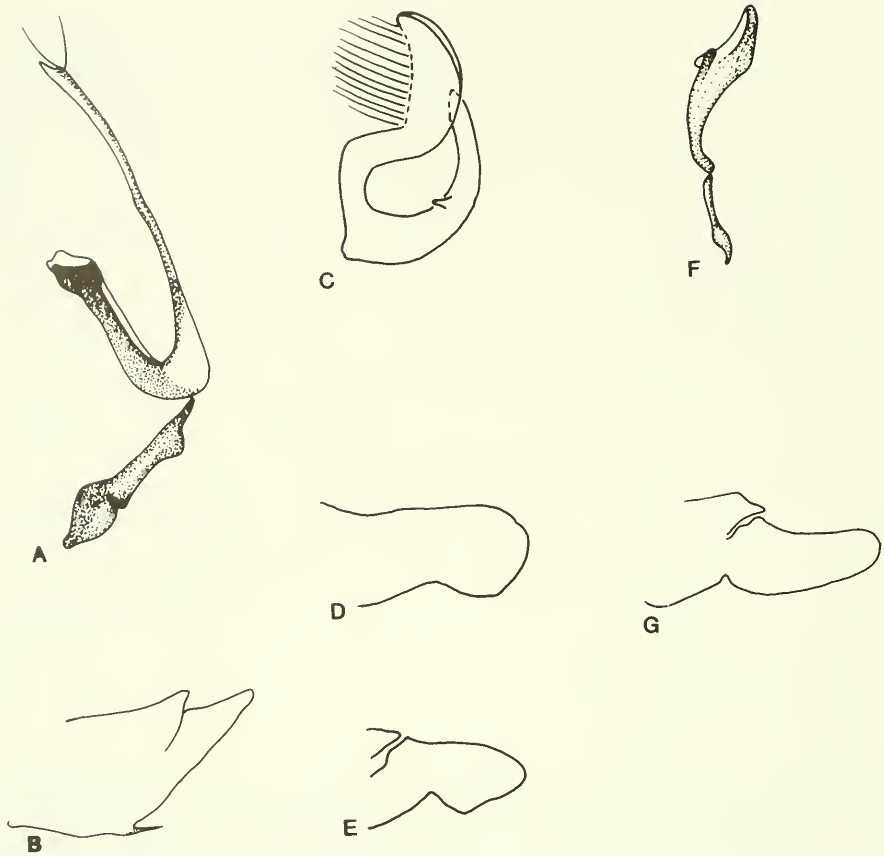


Fig. 55. Male genitalia of genera related to *Flexamia*. *Enantiocephalus cornutus* (Herrich-Schäffer): A, aedeagus and connective, lateral aspect; B, male pygofer, lateral aspect. *Spartopyge mexicana* (DeLong & Hershberger): C, aedeagus, lateral aspect; D, male pygofer, lateral aspect. *Spartopyge miranda* (Knull): E, male pygofer, lateral aspect. *Alapus elongatus* Beamer & Tuthill: F, aedeagus and connective, lateral aspect; G, male pygofer, lateral aspect.

| | |
|---|---|
| *surcula* → *curvata* | [s] Aedeagus with two pairs of processes, one apical, one anteapical (Figs. 7F,G). |
| host = *Buchloë dactyloides* | [au] Apical processes long and not in bilaterally symmetrical plane (Fig. 7F). Gonopore an elongate channel. |
| *zacate* → *canyonensis* | [s] Aedeagus curved, acute apically, without aedeagal processes (Figs. 7I,J). |
| host = *Muhlenbergia porteri* | [au] Gonopore at midlength of aedeagal shaft. |
| *minima* → *zamora* | [s] Style apices in lateral aspect bluntly produced (Figs. 13A,B). |
| host unknown | [au] Outer teeth of female sternum VII incurved, longer than inner teeth (Fig. 14B). |
| *bandarita* → *gila* | [s] Female sternum VII with two produced, median teeth (Figs. 14D,E). Male plates broad, bluntly rounded (Figs. 11D,E). |
| host = *Bouteloua curtipendula* | [au] Male plates nearly as long as pygofer (Fig. 11E). |
| *albida* → *slossonae* | [s] Posterior lobe of male pygofer undifferentiated (Figs. 62Q,T). |
| habitat specialists | [au] Male plates exceed pygofers (Fig. 8B); female sternum VII trilobed (Fig. 10B). Aedeagus and connective partially fused. |
| *picta* → *pyrops* | [s] Aedeagal tip capitate, toothed, with pair of subapical processes (Figs. 7K,L); pygofers (Figs. 5A, B) angulate with ventral process. |
| host = *Aristida* spp. | [au] Vertex extensively produced, anteapical aedeagal processes (Fig. 7L) more remote from apex, male plates (Fig. 9B) very short, rounded. |

| | |
|---|---|
| *arizonensis* → *flexulosa* hosts = *Aristida*/ *Bouteloua gracilis* | [s] Male plates [Figs. 33A,B] short, divergent apically. [au] Apical aedeagal processes short (Fig. 31K). |
| *youngi* → *decora* host = *Muhlenbergia richardsonis* | [s] Unpaired ventral aedeagal processes (Figs. 31F,G) symmetrical and much longer than paired processes. [au] Unpaired process (Fig. 31G) without median groove, aedeagal shaft curved. |
| *celata* → *stylata* hosts = *Redfieldia*/ *Muhlenbergia* spp. | [s] Face (Fig. 3B) with discrete lines forming interocular band; three aedeagal processes angularly divergent from shaft (Figs. 31H,I). Pygofer with distinct posterior process (Figs. 62OO,PP). [au] Apices of male plates subrectangular; aedeagus (Fig. 31H) asymmetrical. |
| *beameri* → *texana* hosts unknown | [s] Aedeagal processes about equal in length, but ventral processes not in sagittal plane (Figs. 31 A,D). [au] Aedeagal processes twisted apically (Fig. 31A). |
| *imputans* → *areolata* hosts = *Muhlenbergia cuspidata*/ *Eragrostis spectabilis* | [s] Unpaired process lateral, with ventral groove (Figs. 31B,C). [au] Aedeagus and connective fused, unique habitus (Fig. 2F). |
| *prairiana* → *reflexa* hosts = andropogonoid grasses | [s] Gonopore dorsal (Figs. 44D,G). [au] Groove absent on unpaired process (Fig. 44D). |
| *sandersi* → *delongi* hosts = andropogonoid grasses | [s] Lateral process appressed to aedeagal shaft (Figs. 44B,C). [au] unpaired process (Fig. 44C) at less acute angle with aedeagal shaft. |
| *satilla* → *clayi* hosts = andropogonoid grasses | [s] Flared, elongate gonopore (Figs. 44H,J). [au] Gonopore broad basally (Fig. 44H). |

*B. Designation of clades*. The next step consisted of appending other species to the sister sets to define clades:

| | |
|---|---|
| *minima* → *zamora* → *pectinata* host probably = *Bouteloua curtipendula* | [s] Style with apical lobe not constricted (Figs. 11A–C); [au] Male plates (Fig. 11C) subrectangular; style tip (Fig. 13C) not produced in lateral aspect. |
| *bandarita* → *gila* → *doeringae* host = *Bouteloua curtipendula* | [s] Middle teeth (Figs. 14D–F) of female sternum VII longer than outer teeth. [au] Middle teeth long, associated to form process (Fig. 14F). |
| *graminea* → *satilla* → *clayi* hosts = andropogonoid grasses | [s] Spiral gonopore (Figs. 44F,H,J) [au] Flared gonopore (Fig. 44H) |

*C. Establishment of species groups*. Clades were next assembled into species groups. These are the groups (I–XIII) described herein. Synapomorphies defining clades and species groups are given in the descriptions to the groups and in the legends to Figures 56–59.

*D. Establishment of polarity between Spartopyge and Flexamia*. The dorsal and facial habitus of *grammica* (Fig. 2C), *albida* (Fig. 2A), and *Spartopyge* (Fig. 54) are clearly homologous. On the other hand, few characters of *grammica* are clearly homologous to those of other *Flexamia* species. The morphology of the male aedeagus and connective places this species in the genus, but the reduced number of aedeagal apices and their apparent phyletic twisting make it difficult to assign homology. The male pygofer and female sternum VII suggest retention of plesiomorphic characters of an ancestor allied to *Spartopyge*. We therefore hypothesize the polarity *Spartopyge* → *grammica*. Derivation of the similarly striped *albida* group, of course, could have occurred only after development of paired aedeagal processes and fusion of the anteapical pair into a single, unpaired process (Fig. 56). Reversing the polarity between *grammica* (or *albida*) and *Spartopyge* would require generation of a wide array of apomorphies present in *Spartopyge*, including a brush of setae on the interior of the pygofer and the complex structures of the male genitalia (Fig. 55C), accompanied by complete loss of all apical processes. Also, the unique sternum VII (Figs. 54D,E) of *S. mexicana* and *S. miranda* would have to arise suddenly. Finally, if *Spartopyge* were derived from the *Flexamia* lineage, it would be necessary to postulate a significant apomorphic increase in size. This would constitute a reversal of the overall trend for size reduction and simplification in the Deltocephalinae in general (Whitcomb et al. 1986) and *Flexamia* in particular. We therefore

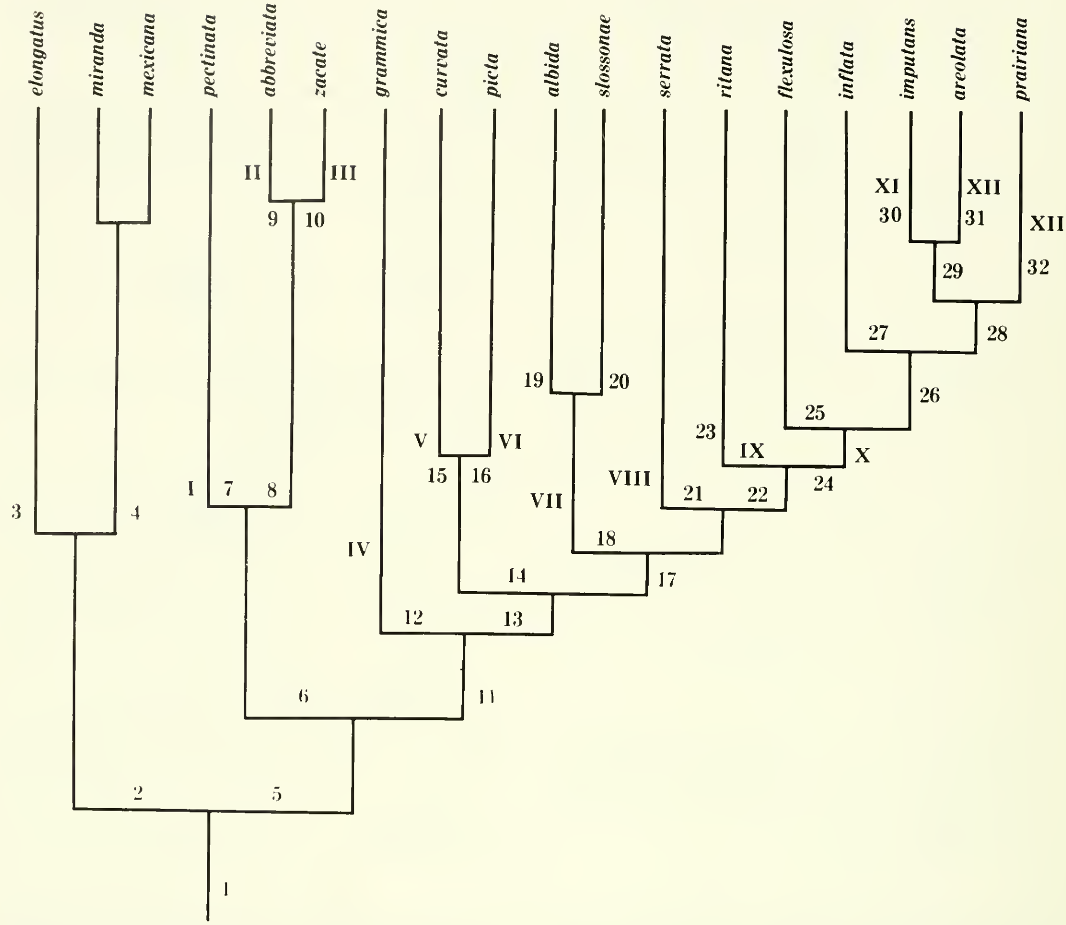


Fig. 56. See facing page.

hypothesize (with Young and Beirne, and Ross) that *Spartopyge* is an outgroup of the *Flexamia* lineage. We believe, with these workers, that a primitive *Flexamia* ancestor arose from the *Spartopyge* lineage and later gave rise to a lineage with paired, aedeagal processes. This lineage in some way gave rise to *grammica* but, ultimately, to all *Flexamia* groups IV–XIII. We assume that the dorsal location of the gonopore in *grammica* and *prairiana* is a result of independent evolutionary events, since these species share few other significant characters. Whether the minute, paired processes that occur midlength on the *Spartopyge* aedeagus are homologous with the *Flexamia* aedeagal processes is conjectural.

PHYLOGENY OF *FLEXAMIA* GROUPS AND SPECIES. The postulated relationships and polarities permit a cladogram to be drawn relating *Flexamia* groups and key species to the outgroups *Alapus* and *Spartopyge* (Fig. 56). Several significant possible variations of the proposed tree are given in Figure 57. Finally, the phylogeny of *Flexamia* species was inferred on the basis of the characters discussed above. We present cladograms for groups I–IX (Fig. 58), groups VII–XI (Fig. 59), and groups XI–XIII (Fig. 60). Synapomorphies used to define clades within each group are given in the legends to the figures.

CHARACTER TRANSFORMATIONS.—Our intuitive phylogeny provided general guidelines concerning character transformation in *Flexamia*. From these concepts we constructed branched transformations for the PHYSYS program of Mickevich and Farris (1984). These transformations, which are described

Fig. 56. Proposed phylogeny of *Flexamia* groups and key species. Synapomorphies [s] or, for monobasic groups, autapomorphies [au] are indicated. We hypothesize an ancestral form (1) that possessed dorsal stripes (Fig. 54A) and a pale face with a contrasting black interocular band (Fig. 54B) similar to those of Figs. 3A and 3B, relatively wide male plates (Fig. 54C); an aedeagus distinctly jointed with the connective, without apical processes, and with an anteapical gonopore on the caudoventral surface. Divergence of this lineage led (3) to *Alapus* (Figs. 55F,G), represented in this diagram by *elongatus*, and to *Spartopyge*, represented (4) in this diagram by *miranda* and *mexicana*, in which [s] the dorsal aedeagal apodeme is large and hoodlike (Fig. 55C). The transformations between *Flexamia* and its outgroups are tenuous (see text). In *Flexamia* [s] the dorsal aedeagal apodeme (Fig. 6) has a pair of conspicuous appendages directed caudoventrad or caudad (5). In the first lineage (6) to diverge, the plesiomorphic aedeagal apex, which lacked processes, was retained, as were the caudoventral position of the gonopore and broad, ancestral plates; the contrasting face was retained in a minority of species, but the striped habitus was completely lost. Synapomorphies defining this lineage include [s] the curved aedeagus lacking processes (Figs. 7I,J; 16A, 17A, 20A) and the male pygofers, which possess both dorsal and ventral constrictions (Figs. 62A–I). This lineage diverged into the *pectinata* (7) and the *abbreviata-zacate* lineages (8). In the *pectinata* group the plates (Fig. 1I) are distinctively parallel-sided basally (except in *collorum*). In the *abbreviata-zacate* lineage the gonopore was at first elongate (Fig. 24) and [s] the posterior lobe of the male pygofer strongly produced (Figs. 62H,I). In the *abbreviata* group (II) the plates (Fig. 8E) are reduced (9), and [au] a distinctive pair of minute apical processes (Fig. 7H) developed. The small aedeagal processes of the *abbreviata* group are not clearly homologous with other aedeagal processes in *Flexamia*. In the *zacate* group (III) the gonopore (Fig. 24) was at first elongate (10) but in *canyonensis* moved to the aedeagal midpoint. At this point a significant apomorphy appeared. An ancestral form (11) is hypothesized in which two pairs of aedeagal processes were present. It is unclear whether this form had fully developed before divergence of *grammica* (IV), in which the plesiomorphic feature of dorsal stripes was retained (12), but in which [au] the aedeagal processes were distinctively modified (Fig. 7E) and the gonopore had moved to the dorsal surface (12). A possible apomorphy linking *grammica* with the *curvata* group is the foot-shaped style apex (see illustrations of Young and Beirne 1958). In the *curvata-picta* lineage [s] both pairs of aedeagal processes are present (14), but many habitus features, including stripes and contrasting face, have been lost. In the *curvata* group (V) two pairs of processes are present (15) and [s] unmodified (Figs. 7F,G). In the *picta* group (VI) the apical processes are [s] modified (Figs. 7K,L) as flangelike, toothed appendages (16). Remaining species are defined by an apomorphy that developed with the presumed fusion (17) of the anteapical processes into a single, unpaired process that was plesiomorphically located ventrally in the sagittal plane (Figs. 31, 61A). A second apomorphy characterizing this divergence is the bifurcation (Figs. 7A–C) of the apical aedeagal processes, a feature that was subsequently lost (22). The plesiomorphic state of dorsal stripes and contrasting face was preserved (18) during the fusion of subapical processes and is present (Figs. 2A,B) in the *albida* group (VII). This lineage, which can be defined [s] in terms of the absence of dorsal or ventral constrictions in the posterior lobe of the male pygofer (Figs. 62Q,T), is represented today by the distantly related sister species *albida* (19) and *slossonae* (20); for autapomorphies defining these species, see text. In *serrata* (VIII) [au] additional dorsal aedeagal processes (Fig. 7A) developed (21), and, while the contrasting face was retained, dorsal stripes were lost (Fig. 1). In *ritana* (IX) the dorsal stripes were retained (Fig. 2D) but greatly reduced. This monobasic group (23) is defined [au] by the unique, pointed aedeagal apex (Fig. 7D). In one lineage of the *flexulosa* group (25), the unpaired aedeagal process is, plesiomorphically, ventral in the sagittal plane, permitting retention of aedeagal symmetry (Figs. 31G,I,J,K,L). The plesiomorphic pale face with black interocular band (Figs. 3B,F,G) was also retained. This clade is defined [s] by the triangulate plates (Figs. 33A–F, 34D) with conspicuous, apical divergence. (But in *stylata* [Fig. 34E], the plates [au] are truncated.) In the remaining species (26) the unpaired process underwent phyletic twisting (Figs. 61B–H) and the contrasting pale face, which had persisted through many nodes, was finally lost. In the *inflata* subgroup of group X, [s] the displacement of the unpaired process (Fig. 61B) was relatively small (27), but [s] in the *imputans-areolata* (XI-XII) lineage the process had become lateral (Figs. 31B,C) and bore the gonopore as an elongate slit (29). Before divergence of groups XI-XIII, the connective and aedeagus had remained articulated (but see discussion of group VI in text). We hypothesize that after divergence of the *imputans-areolata* lineage, a fusion of aedeagus and connective occurred (31) in *areolata*. The *imputans-areolata* lineage is very specialized in the location of the unpaired process, in the black face, and the greenish dorsal pigmentation. Of the two species, *areolata* is the more highly specialized (Figs. 2F, 10Q); in fact, it may be the most highly specialized of all *Flexamia* species. It is most unlikely that the widely distributed and variable *prairiana* (see text) and the entire *prairiana* group (XIII) were derived from the specialist *areolata* lineage. Instead, we propose that divergence of a second lineage in which aedeagus and connective fused (32) led to the *prairiana* group. This fusion, the traces of which are evident (Fig. 6F) in *prairiana*, is designated [s] as a synapomorphy defining group XIII, and the fusion in *areolata* is defined as an autapomorphy defining that species. Details of species phylogenies are presented in detail in Figures 58–60.

in Appendix II, Part III, involved the following characters: (1) relationship between aedeagus and connective; (2) morphology of the aedeagal apex; (3) morphology of anteapical aedeagal processes; (4) phyletic twisting of the unpaired ventral process (Fig. 61); (5) curvature (lateral aspect) of the aedeagus; (6) thickness (lateral aspect) of the aedeagus; (7) length of the aedeagus; (8) form of the aedeagal shaft; (9) form of margins of paired, aedeagal processes; (10) form and position of the gonopore; (11) morphology of apices of the apodemal arms; (12) position of apodemal arms; (13) width of dorsal keels of the connective; (14)

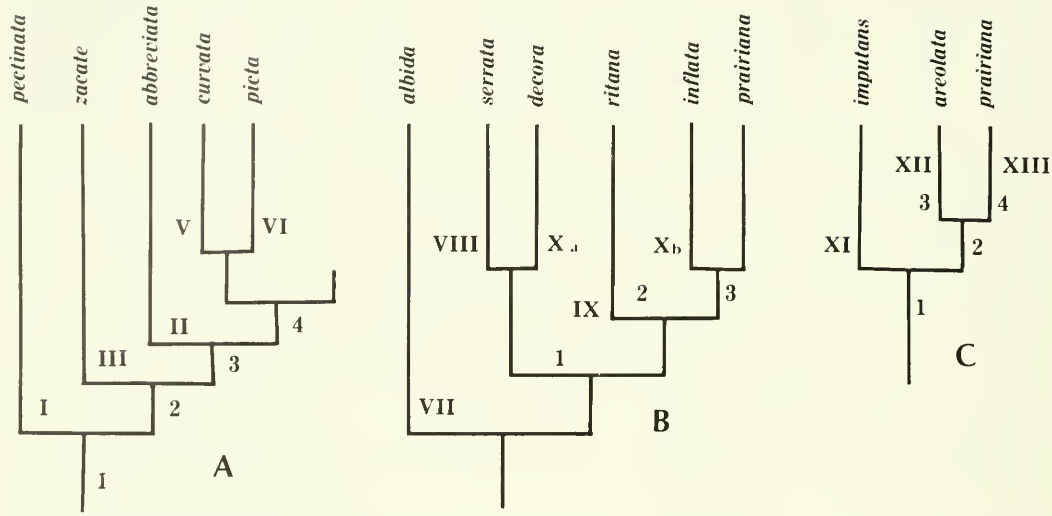


Fig. 57. Alternative resolutions for *Flexamia* group phylogenies. A. In this resolution (1) two groups (I and III) are defined by [s] curved aedeagus without processes (Figs. 7I,J, 16A, 21A). The alternative lineage (2) is defined by an apomorphic elongation of the gonopore. This was followed by derivation of a further lineage (3) in which aedeagal processes are present. At first these are [s] minute (II *abbreviata*, Fig. 7H) but later become (4) fully developed (see Figure 56). This resolution avoids hypothesizing independent origins for the aedeagal processes in *abbreviata* and *curvata* but hypothesizes additional nodes between *Spartopyge* and the *Flexamia* species with very similar habitus, implying repeated, independent losses of the complex pattern of striping in *Spartopyge*, *grammica*, and *albida*. B. In this resolution, it is hypothesized (1) that the *serrata* group and *decora* subgroup of group X belong to a common lineage, and that the *inflata* subgroup of group X is more closely related to *ritana*. This construction has considerable merit and takes into account the similarities between the *serrata* male plates (Fig. 8C) and those of the *decora* subgroup (Figs. 33, 34D,E), but deemphasizes many similarities between members of the *inflata* and *decora* lineages, and would augur for elevation of these lineages to groups. C. It is possible to hypothesize a single (2) fusion of aedeagus and connective, rather than the two fusions hypothesized in Figure 56. This construction, in our view, gives insufficient weight to several synapomorphies that link *areolata* and *imputans*, which would, in fact, have been designated as a close sister species set had they not differed in the crucial relationship of aedeagus to connective. See discussion in legend to Figure 56, and text.

morphology of the male pygofer (Fig. 62); (15) morphology of the male plates; (16) morphology of the female sternum VII; (17) presence or absence of dorsal stripes; (18) coloration of the face.

The above transformations, as presented in Appendix II, are suitable for entry into the PHYSYS program and should serve as a useful starting point for more refined analysis of *Flexamia* phylogeny.

SUMMARY OF PHYLOGENETIC MODEL.—In summary, after numerous iterations, we propose a formal phylogeny for *Flexamia*. The model is rooted in earlier informal work of Young and Beirne (1958) and Ross (1970, and unpublished notes). Our model, in addition to its formality, considers 14 species not available to earlier workers and proposes species groupings based in large part on synapomorphies. In particular, the addition of seven species to the *pectinata* group (I) and four species to the *flexulosa* group (X) adds new phylogenetic perspectives.

We have accepted the hypothesis of Young and Beirne of an ancestral form with two pairs of aedeagal processes. We also endorse the proposal of Young and Beirne (and Ross) that the anteapical pair of processes fused to form a single, unpaired process (Fig. 52). Further, we accept the proposal of Ross (Fig. 53) that the fusion of aedeagus and connective is an important synapomorphy that defines the *prairiana* group.

The informal proposal of Ross differed from that of Young and Beirne in one major way (in addition to its presentation as a tree). Ross believed that the lack of aedeagal processes in *pectinata* and *canyonensis* was plesiomorphic and related it to the similar lack of processes in his outgroups, *Spartopyge* and *Aflexia*. In our

proposal we have sided with Ross. Unless different outgroups were chosen, we feel such an assignment is inevitable. Also, transformations within *Flexamia* are best explained by the chosen polarity. For example, viewing the *pectinata* group as the terminus of a simplification of the aedeagus would require the transformation of male plates from narrow to broad, in direct contrast to the general tendency for streamlining of the plates that runs throughout the remainder of the *Flexamia* tree.

We have assumed, with Ross, that the minute processes in *abbreviata* are not homologous with other *Flexamia* aedeagal processes. This assumption, which permits many other reasonable character transformations to be postulated, appeared in our model only after numerous iterations failed to find a better resolution, considering all transformations. Such issues are best addressed by close examination of the structures themselves, preferably by scanning electron microscopy, for evidence that would bear on the question of homology. It is possible that a computerized search for a parsimonious tree would turn up a cladogram that avoids the pitfalls we encountered in our intuitive search. In any event, we present in Figure 57A an alternative cladogram that, whatever its other problems, assumes homology between the aedeagal processes of *abbreviata*, *grammica*, and *curvata*.

Young and Beirne (1958), although uncertain about the status of *dakota*, *atlantica*, and *grammica*, nevertheless placed them tentatively in their lineage IIIB (Fig. 52). We concur with Ross in his placement of *dakota* and *atlantica*. However, we disagree with both Young and Beirne and Ross in the placement of *grammica*. Whereas the dorsal location of the gonopore and the presence of two serrate, aedeagal processes of this species is clearly highly apomorphic, we see nothing else in *grammica* that links it to group XIII, in which the dorsal location of the gonopore is a significant apomorphy. For example, the male plates and pygofers, the female sternum VII, the clear articulation of aedeagus and connective, the striped habitus and pale face, and the overall large size of *grammica* are derivable as transformations from the outgroup *Spartopyge*, but they would produce chaos if inserted into transformations in group XIII (or any other group or groups between VII and XII). In fact, the ties between *Spartopyge* and *grammica* are sufficiently reasonable that we have couched our argument for the polarity *Spartopyge* → *Flexamia* in terms of *grammica* (see earlier section).

The model we present solves many of the problems that we encountered. Resolution of many questions was made possible by proposing (1) that aedeagal processes arose in the course of *Flexamia* evolution and were not inherited from an unknown ancestor; (2) that aedeagal symmetry was plesiomorphic (but note the apomorphic symmetry in *dakota*). Further character transformations have been proposed (Appendix II, Figs. 61, 62) that lead to consistent hypotheses for transformation of other characters (e.g., bases of the first valvulae, which are presented in Fig. 63 in terms of our proposal but were not used to derive it). The proposed resolution avoids hypothesizing independent acquisitions of the unique striped habitus present in *Spartopyge*, and in *grammica*, *albida*, and *slossonae*. It further avoids hypothesizing independent derivations of the unique facial habitus of the outgroup, which was retained through a considerable segment of *Flexamia* evolution. We do hypothesize several independent losses of these distinctive sets of habitus characters. Finally, the proposed model follows the following general polarities: (1) tropical grasslands → subtropical grasslands → temperate grasslands → [semiarid grasslands, prairie]; (2) large → small size; (3) grass generalist → chloridoid specialist → mixed chloridoid-panicoid specialist → andropogonoid specialist; (4) striped habitus → [light habitus (semiarid), brown (prairie)]; and (5) aedeagal symmetry and caudoventral gonopore → highly specialized aedeagal configurations and gonopore locations.

But not all the problems have been solved. We regard the cladogram for groups I–III to be tentative. The position of *mescalero* as a member of group I is unclear; this unique species might have been more appropriately considered to be a separate group linking groups I and III. In fact, the general question of polarity of the *pectinata* group should be critically addressed. We are not certain how to interpret evidence of considerable recent speciation in this group (i.e., *bandarita*/*gila*, *minima*/*zamora*/*pectinata*). It is likely, given our

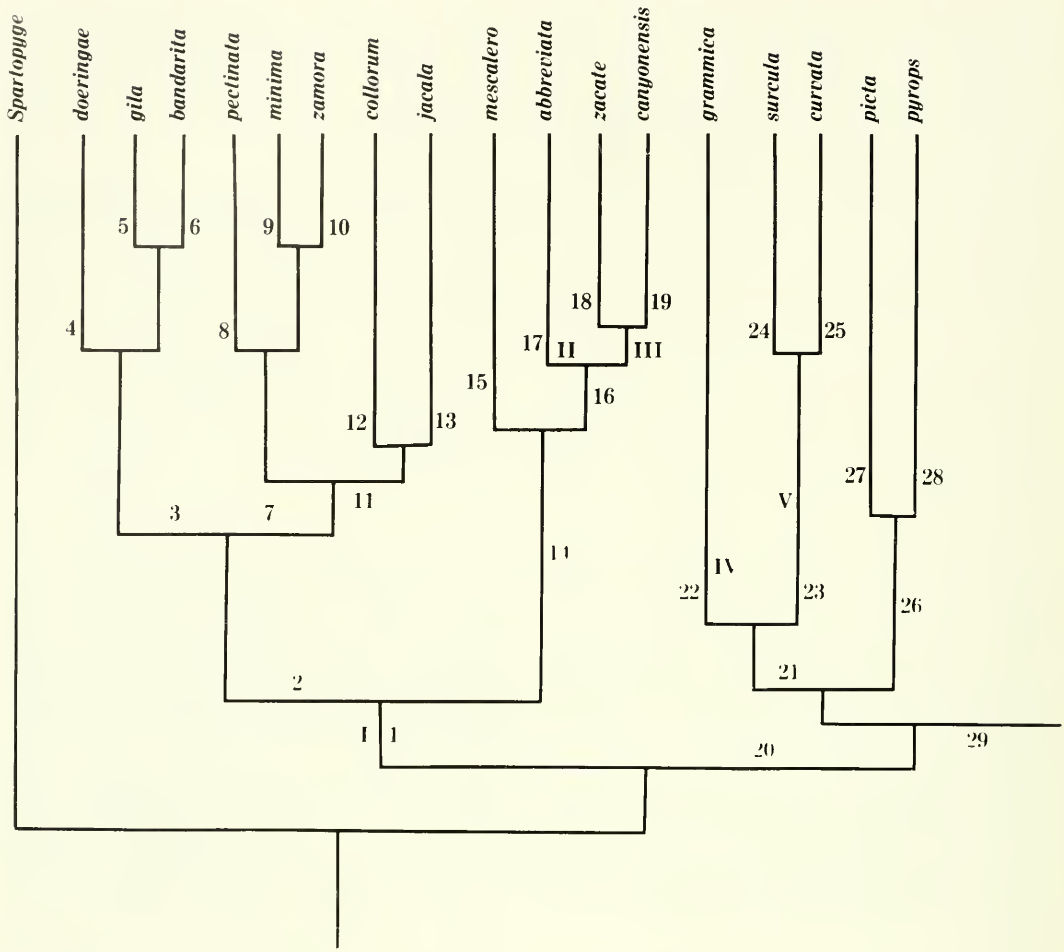


Fig. 58. See facing page.

discovery of many new species from the Southwest, that further acquisitions of *Flexamia* or related genera from Mexico may change our perceptions dramatically. Also, a wider selection of outgroups would clarify the status of the early *Flexamia* lineages.

Young and Beirne (1958) proposed that grooves on the unpaired aedeagal process were vestiges of a plesiomorphic condition in which the halves of the processes were separate. This condition occurs in several species (*youngi*, *imputans*, *prairiana*), but we have been unable to link these species in any transformation that is consistent with other transformations.

Finally, we propose, with some confidence, that the articulation between aedeagus and connective was subject to fusion or partial fusion in four nodes of our model. These were in the lineages leading to *picta-pyrops*, to *areolata*, to *slossonae*, and to the *prairiana* group. Given the different products of each of these fusions, and the position on the tree in which they occurred, we have no problem in treating each as a synapomorphy.

The genus *Flexamia* is rich in characters and should provide an excellent model for the PHYSYS program. It is likely that careful study and numerous iterations using such a program will further improve phylogenetic hypotheses concerning *Flexamia*.

## BIOGEOGRAPHIC IMPLICATIONS OF THE PHYLOGENETIC MODEL

Ross (1965, 1970) felt that many speciation

Fig. 58. Phylogeny of species of groups I-IX. The following events, including synapomorphies [s] and autapomorphies [au] are postulated: (1) In the plesiomorphic state of the *pectinata-abbreviata* subtree, the male plates were broad (Fig. 11), the male pygofers constricted (Fig. 62F), the gonopore oval on the caudoventral surface, and the aedeagus (Figs. 12A–H) without apical processes; (2) in one subtree of the *pectinata* group (comprising eight of its nine species), the aedeagal tip remained unmodified but flared (Figs. 12A–H). In all three species of the *gila* division (3) of this group, the female sternum VII developed [s] long, median, paired teeth (Figs. 14D–F); in *doeringae* (4) these teeth [au] became associated into a medial process (Fig. 14F). In *gila* (5) [au] the male plates are elongate (Fig. 11E), in *bandarita* (6) [au] shortened (Fig. 11D). Evolution of this cluster, of *pectinata*, and, perhaps also of *minima* and *zamora*, occurred on *Bouteloua curtipendula*. The three species of the *minima* cluster are defined [au] by (8) subrectangular plates (*pectinata:* Fig. 11C), (9) short plates (*minima:* Fig. 11A), and (10) outer teeth of hind margin of female sternum VII longer than median teeth (*zamora:* Fig. 14B). Divergence from this cluster (11) involved [s] development of avicephaliform style tips. In *collorum* (12), which appears to be a specialist of *Bouteloua uniflora*, a close relative of *B. curtipendula*, [au] the plates (Fig. 11G) are extremely short. In *jacala* the plates (Fig. 11H) remained long and broad (13); this is the only *Flexamia* species with both long, broad plates and avicephaliform style tips. In another species cluster a tendency toward development of aedeagal processes developed. In *mescalero* (15) [au] the aedeagus (Fig. 22) is slightly capitate rather than flared. This specialist of *Muhlenbergia pauciflora* retained relatively broad plates (Fig. 11I) and constricted pygofers (Fig. 62B) typical of the *pectinata* group; we therefore regard it as a monobasic subgroup of group I. A monophyletic cluster of three species is presumed to have arisen (16) from this lineage. Each of these species has [s] a pygofer with a conspicuously produced posterior lobe (Figs. 62H,I). In *abbreviata* (group II) the aedeagal apex [au] bears (Fig. 7H) two minute, paired processes (17). In this species and in *zacate* (18) the gonopore (Fig. 24) is elongate. *F. zacate* is the only species of the genus that lacks aedeagal processes but has an elongate gonopore. In *canyonensis* the gonopore [au] is located (19) approximately at the midpoint of the aedeagal shaft, presumably as a consolidation of the elongate gonopore type of *zacate*. The shape [au] of the aedeagal shaft in *canyonensis* (Fig. 6C) is also unique. The sister species *zacate* and *canyonensis* are both specialists of *Muhlenbergia porteri*. In a very important divergence (20), development of two pairs of aedeagal processes is hypothesized. In *grammica* (22), a *Calamovilfa* specialist, the plesiomorphic habitus of the *Spartopyge* dorsum and face were retained. Two of the four hypothesized aedeagal processes may have been lost. The pygofers and male plates also suggest relationships with *Spartopyge*, but in contrast to this outgroup, aedeagal processes are present. The relationship of *grammica* to other *Flexamia* species with aedeagal processes is unclear, given the [au] specific asymmetry of these processes (Fig. 7E) and the location of the gonopore, which has moved to a dorsal position. It is possibly significant [s?] that the style apices of the *grammica* and *curvata* groups are foot-shaped (21). In the *curvata* set (23) of sister species (*Buchloë* specialists) [s] two pairs of processes are present. In *curvata* (25) [au] the gonopore is elongate. In the *picta* lineage (*Aristida* specialists) two pairs of processes are present but [s] the apical pair has been modified into flangelike, toothed structures (26). Several autapomorphies [au] characterize (28) *pyrops* (see text). From this subtree the remaining species of *Flexamia* were derived; this derivation was featured (29) by an apomorphic fusion of the anteapical pair of processes into a single, unpaired process located on the ventral surface of the aedeagus in the sagittal plane.

events involving phytophagous insects could be explained by host transfer; the genus *Flexamia* was one of the genera that he chose for the study of host choice and speciation in the Cicadellidae. Ironically, Ross happened to work largely in central, northern, and southeastern grasslands. In these regions the study of cicadellid host relationships is more difficult than in the Southwest, and, as it turned out, almost all of the undescribed species in the genus occurred outside the geographic regions in which he conducted his extensive fieldwork.

Today, in retrospect, we report that the choice of *Flexamia* was a wise one; however, fewer speciations appear to be due to host transfer than Ross might have predicted. Sister species have in many cases proved to be specialists of the same host or closely related hosts. Indeed, entire groups of species have proved to have similar (often congeneric) patterns of host selection.

The progression of evolutionary divergence in *Flexamia* can best be described in terms of the phylogeny we propose. In Figures 64–67 we illustrate the postulated biogeographic and host transfer events.

We believe that the most closely related outgroup is *Spartopyge*. We have no information on the host relationships of *mexicana*, but *miranda* occurs on *Bouteloua curtipendula* in Arizona. The general facies of *Spartopyge* appears to be homologous with that of some *Flexamia* groups (*albida*, *grammica*, and *ritana* groups). We propose that diversification of the *Spartopyge* lineage in Mexican grasslands led to *Alapus* and to *Flexamia*.

We propose that the initial divergence (Fig. 65) of the *Flexamia* lineage resulted from specialization of a generalist ancestor on side-oats grama, *Bouteloua curtipendula*. This lineage, influenced by host patchiness and/or regional climatic differences, diverged by dispersal or vicariance into at least six species. These are

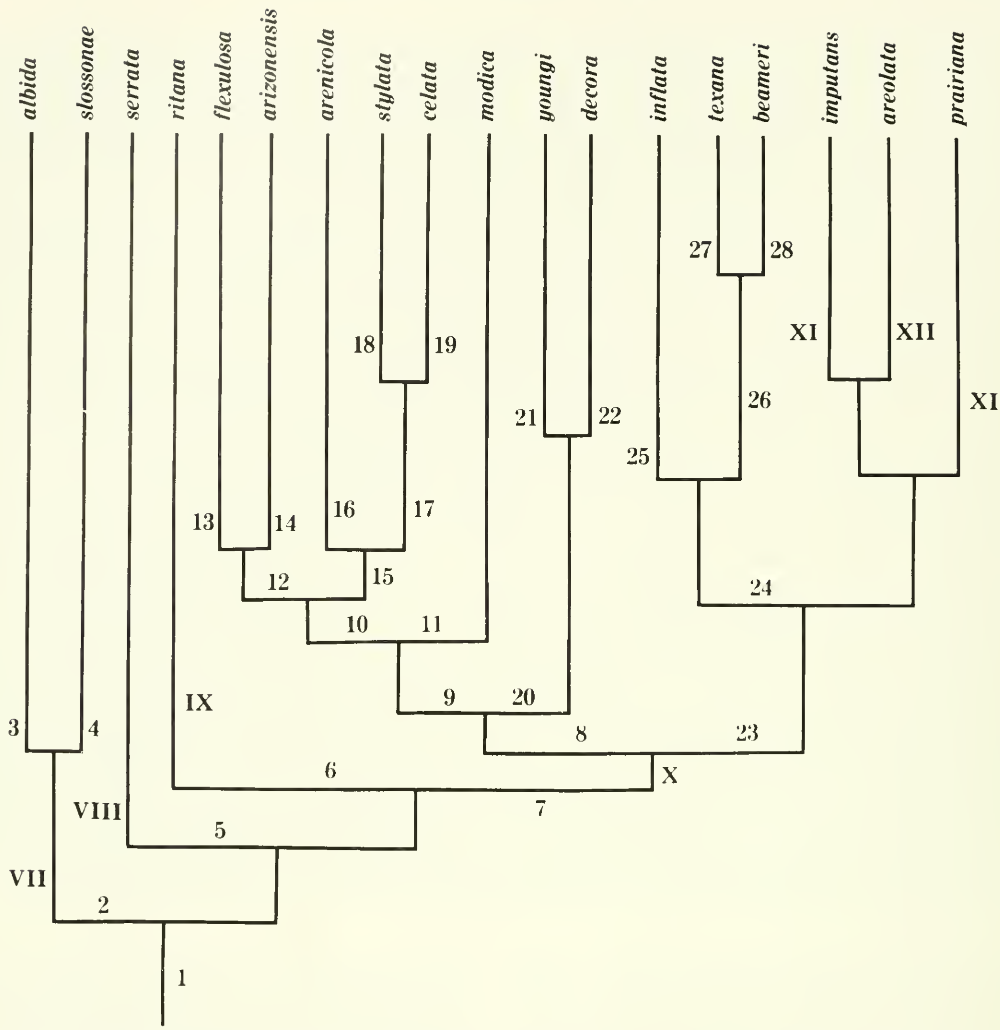


Fig. 59. Phylogeny of species of groups VII-XI. The following events, including synapomorphies [s] and autapomorphies [au] are hypothesized. Plesiomorphically, this cluster retained (1) certain features of the *Spartopyge* habitus (i.e., dorsal stripes and a pale face with black interocular band). However, prior to divergence, two pairs of aedeagal processes had developed, and, subsequently, the anteapical pair had fused to form a single, unpaired ventral process (Figs. 7A–C, 31). The lineage diverged into the (2) *albida* (VII), (5) *serrata* (VIII), and (6) *ritana* (IX) groups. The relationships of these groups is discussed in the legend to Figure 56. A large clade that then diverged (8) was associated mainly with *Muhlenbergia*. In all species of this subgroup the plesiomorphic character of a pale face with black interocular band was retained, but the dorsal stripes were lost. The subgroup is defined [s] by the triangulate male plates (Figs. 33A–F, 34D,E), which are strongly divergent apically (but see *serrata* [Fig. 8C]; the plates of this species suggest a link to the *decora* subgroup). In the *youngi* sister species set (host: *Muhlenbergia richardsonis*), the unpaired ventral process (Figs. 31F,G) retained its plesiomorphic position and length (20), but in the remaining species [s] the process was shortened (9). In *modica* the aedeagus is subsymmetrical (11) with [au] the short, unpaired process (Fig. 31M) slightly displaced from the sagittal plane and associated with the shaft basally; the pygofer is relatively undifferentiated. In the lineage that diverged subsequently, the pygofer (Fig. 62) became substantially modified (10). We hypothesize that it first became ovate, a condition that still persists [au] in *arenicola* (16). In *stylata* and *celata* [s] it developed [s] a distinctive posterior process (17: see text for further synapomorphies), and in *arizonensis* (au) it developed a conspicuous ventral process (14). The male plates of *flexulosa* and *arizonensis* (Figs. 33A,B) are in each case (13, 14) distinctive [au]. In the *inflata* subgroup of group X (24), the beginning of phyletic torsion of the aedeagus is evident (Fig. 61B). In this subgroup the face is modified; traces of the interocular band are present in some individuals, but, when present, it is brown and contrasts much less sharply with the remainder of the face. The plates are short, and [s] the dorsal margin of the pygofer is essentially flat, giving the pygofers a boatlike outline in lateral aspect (Figs. 62GG,HH,II). Two apparent (but see text) sisters, *texana* and *beameri*, are identified by [au] unique aedeagal configurations (Figs. 31A,D). From the moderately displaced aedeagus of the *inflata* group, further torsion (29) led to groups XI-XIII.

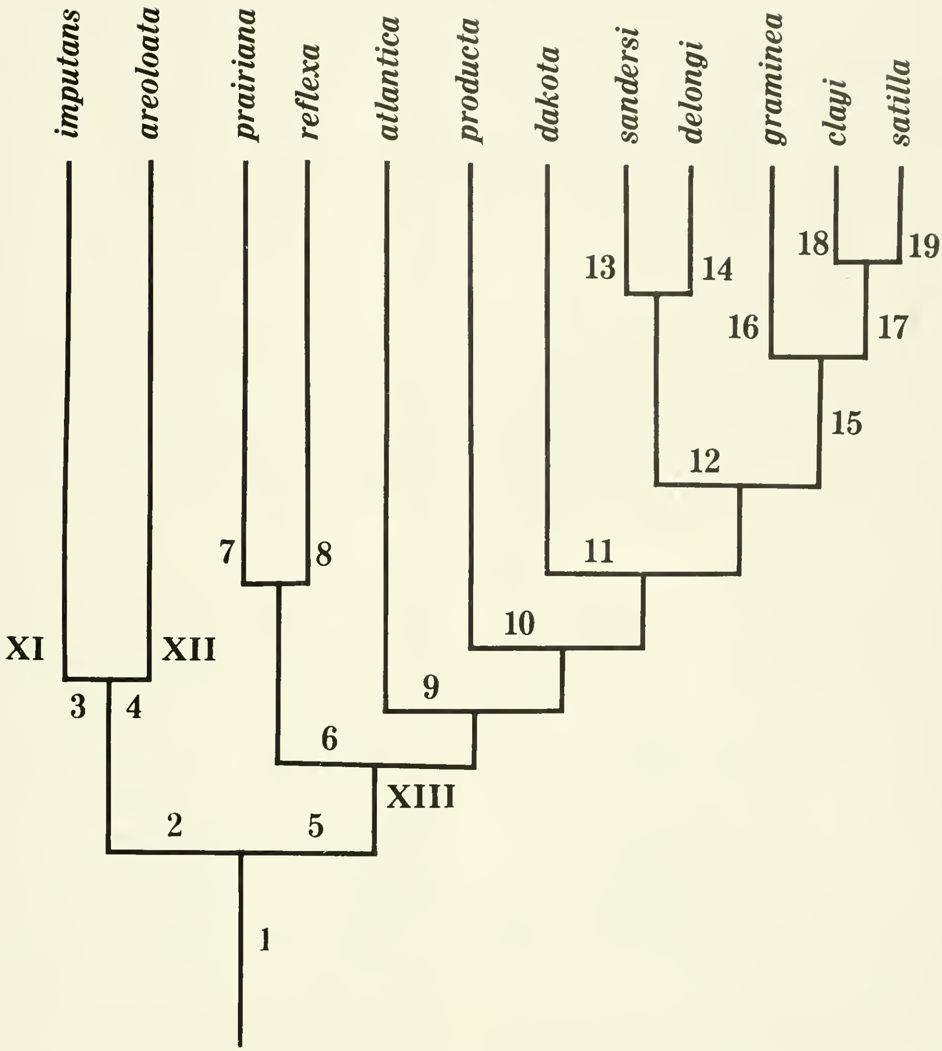


Fig. 60. Phylogeny of species of groups XI-XIII. Synapomorphies [s] and autapomorphies [au] are identified. In the plesiomorphic state (1) there may have been moderate aedeagal asymmetry, as in *inflata* (Fig. 61B). In the *imputans-areolata* lineage (2) [s] the unpaired processes are lateral, bearing a slitlike gonopore (Figs. 31B,C). In *imputans* (3) the ancestral articulation between aedeagus and connective was retained. This unique species is defined by a suite of apomorphies, including its black face, greenish dorsal pigmentation, and lack of dorsal markings, but lacks an autapomorphy. In *areolata* (Fig. 61C) [au] the aedeagus and connective have fused, and a conspicuous, black spot (Fig. 2F) is present in the corium (4). Because the *imputans* and *areolata* lineage is defined by several synapomorphies (see text), we have designated them as sister species, despite the important difference in the state of articulation between the aedeagus and connective. We hypothesize a second, independent fusion of aedeagus and connective that serves as a synapomorphy [s] defining group XIII (4). In the *prairiana-reflexa* lineage [s] the gonopore has become dorsal (Figs. 61D,E), as has the unpaired process (6). In *prairiana* (7) the traces of this fusion [au] are present as a transverse line (Fig. 6F) on the surface of the aedeagal shaft. The aedeagal configuration [au] is also unique (Fig. 61D). In *reflexa* (8) the gonopore [au] has become associated with the unpaired process (Fig. 61E). In *atlantica* one process has been lost, and [au] the aedeagus (Fig. 44A) has become highly asymmetrical (9). In *producta* [au] the gonopore has moved (10) to a lateral position (Fig. 61G), whereas in *dakota* (11) the gonopore remained dorsal (Fig. 44I), but the unpaired process has been lost. The symmetry of the *dakota* aedeagus is therefore apomorphic. In the *sandersi-delongi* lineage (12) the unpaired process has been retained but is present [s] as a lateral process that is closely appressed to the aedeagal shaft (Fig. 61F). In all three species of the final lineage (15), the unpaired process has essentially disappeared; instead, [s] the gonopore has become spiral, with [au] a narrow, basal portion (Fig. 44F) as in *graminea* (16), or [s] with a wider base (17) as in *clayi* and *satilla* (Figs. 44H,J). For discussion of the minor morphological divergences that define the sister species of the *sandersi-delongi* and *clayi-satilla* sets, see text.

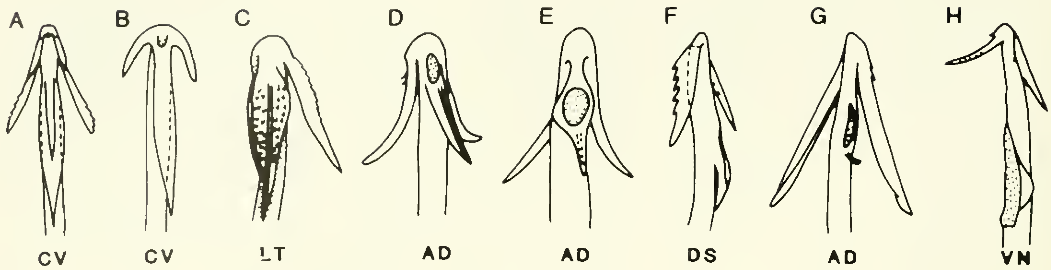


Fig. 61. Postulated character transformation: phyletic twisting and modification of the *Flexamia* aedeagus. In *decora* (A) a plesiomorphic state exists in which the unpaired process is ventral and in the sagittal plane; the aedeagus is therefore symmetrical. In *inflata* (B) there is a small displacement of the unpaired process. In *areolata* (C) the unpaired process is lateral and bears the gonopore. In *prairiana* (D) the process is dorsal, as is the gonopore. In *reflexa* (E) the gonopore has become associated with the dorsal unpaired process. In *sandersi* (F) the unpaired process is reduced and appressed to the shaft. In *producta* (G) the process is reduced or absent and the gonopore is lateral. In *graminea* (H) the process has disappeared entirely, the apical processes are reduced, and the gonopore is spiral. Aspects: AD, anterodorsal; CV; caudoventral; DS, dorsal; LT, lateral; VN, ventral. Aedeagal structures redrawn from Young and Beirne (1958).

adapted to northeastern (*minima*) and west central (*zamora*) Mexican grasslands, to Chihuahuan (*bandarita*) and Sonoran (*doeringae*) montane grasslands of the Southwest, to the interdesert montane region of the Gila Mountains (*gila*), and to the tall-grass and mixed-grass prairie of the United States (*pectinata*). Also derived from the side-oats lineage were *jacala* (Mexico: host unknown) and *collorum* (Edwards plateau; host: *Bouteloua uniflora*), a close relative of side-oats grama). Clearly, most or all of the nodes in the *pectinata* lineage are Mexican or southwestern; none represent events that assuredly took place north of the Mexican–U.S. border.

A second lineage of the *pectinata* subtree resulted in the divergence of *mescalero*, a distinctive species that represents a host transfer to New Mexican muhly, *Muhlenbergia pauciflora*. Another branch of this lineage transferred to temperate *Bouteloua* grasslands of Mexico. One of the branches (*abbreviata* group) inhabited the mixed *Bouteloua* grasslands of Mexico and, by gradual adaptation, to similar grasslands of the United States. Another branch adapted to semiarid grasslands by colonizing bush muhlenbergia (*Muhlenbergia porteri*); divergence of this lineage led to the contemporary *canyonensis* (Sonoran) and *zacate* (Chihuahuan).

Consider next the *surcula-curvata* lineage. Both species possess the four aedeagal processes that Young and Beirne proposed as plesiomorphic; both species are *Buchloë* specialists. We propose that an ancient Mexican ancestral line adapted to *B. dactyloides*, which led to the present-day *surcula* and, later, to *curvata*. This divergence (Fig. 64) may have been mediated by climate. The grasslands of northeastern Mexico, where *surcula* may have arisen, have escaped major disturbance since the Cretaceous (Rosen 1978). This region has an extremely warm, temperate or subtropical climate and a Chihuahuan precipitation pattern, both of which differ immensely from the dry, temperate grasslands where *curvata* occurs today.

Another branch of the *curvata* subtree diverged, perhaps in Mexico or south Texas, leading to the *picta-pyrops* sister set. These species are *Aristida* specialists.

One of the major events in *Flexamia* phylogeny was marked by the fusion of the anteapical pair of aedeagal processes into a single, mesal process. The most primitive species in which this feature is retained are members of the *albida*, *serrata*, and *ritana* groups. Young and Beirne argued (and Ross concurred) that *slossonae*, *albida*, and *serrata* were related. We agree but consider their divergence to be an ancient one, given their entirely different climatic requirements (subtropical, prairie, and northern grasslands, respectively), and their retention of the *Spartopyge* habitus type. Perhaps the divergence of the *albida* lineage into four species, each with unique climatic adaptations, may have occupied a distinct stage in *Flexamia* evolution.


Fig. 62. Character transformation of the *Flexamia* pygofer. Diagrammed lineage was based in part on phylogeny of groups (see Figure 56). A, *collorum;* B, *mescalero;* C, *bandarita;* D, *jacala;* E, *gila;* F, *pectinata;* G, *doeringae;* H, *abbreviata;* I, *canyonensis;* J, *pyrops;* K, *curvata;* L, *surcula;* M, *picta;* N, *Spartopyge miranda;* O, *grammica;* P, *serrata;* Q, *albida;* R, *Alapus elongatus;* S, *Spartopyge mexicana;* T, *slossonae;* U, *ritana;* V, *imputans;* W, *prairiana;* X, *reflexa;* Y, *atlantica;* Z, *areolata;* AA, *producta;* BB, *dakota;* CC, *sandersi;* DD, *clayi;* EE, *graminea;* FF, *decora;* GG, *inflata;* HH, *texana;* II, *beameri;* JJ, *modica;* KK, *youngi;* LL, *arenicola;* MM, *arizonensis;* NN, *flexulosa;* OO, *stylata;* PP, *celata*. Some pygofers were redrawn from Young and Beirne (1958) and Lowry and Blocker (1987).

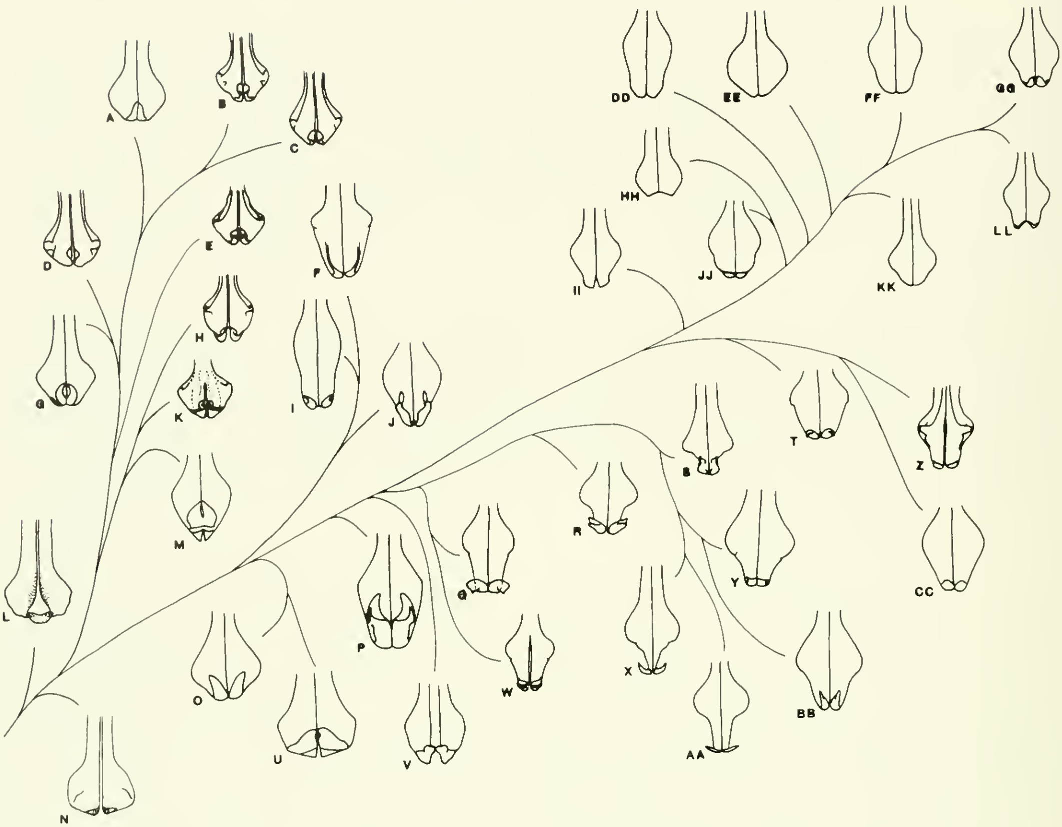


Fig. 63. Bases of first valvulae of *Flexamia* species. The depicted tree represents phylogeny presented in Figures 56–60. A, *doeringae;* B, *gila;* C, *bandarita;* D, *collorum;* E, *mescalero;* F, *curvata;* G, *pectinata;* H, *canyonensis;* I, *surcula;* J, *picta;* K, *zacate;* L, *Alapus elongatus;* M, *abbreviata;* N, *Spartopyge mexicana;* O, *albida;* P, *serrata;* Q, *decora;* R, *modica;* S, *arenicola;* T, *inflata;* U, *slossonae;* V, *ritana;* W, *youngi;* X, *celata;* Y, *arizonensis;* Z, *beameri;* AA, *stylata;* BB, *flexulosa;* CC, *texana* ;DD, *atlantica;* EE, *producta;* FF, *sandersi;* GG, *clayi;* HH, *reflexa;* II, *imputans;* JJ, *prairiana;* KK, *dakota;* LL, *graminea*.

Interestingly, there are present-day clues to the feeding strategies of this primitive complex. We suspect that *slossonae* and *albida* are habitat specialists, whereas *serrata* specializes on *Muhlenbergia richardsonis*. Ancestral *Flexamia* species in Mexican grasslands may have been general grass feeders; this strategy has been partially retained by some lineages, including those that retained the plesiomorphic striped habitus.

Perhaps the striped habitus is optimal for habitat specialists. Loss of the habitus occurred homoplastically several times; in at least one case (*serrata*), it accompanied host specialization in northern, temperate grasslands (on *Muhlenbergia richardsonis*). This event could actually have taken place far south of the current range of *serrata* during a glacial maximum in the early Pleistocene. *Muhlenbergia richardsonis* not only occurs as far north as Wood Buffalo National Park in Canada, but also occurs in Mexico, presumably as a relict. Throughout much of the northern part of its range, this warm-season grass is an "island" surrounded by a sea of cool-season grasses. Such a condition is ideal for evolution of a specialist lineage from a more general ancestor; taxonomic distinctiveness has been recognized as an important force in determining insect species richness on plant hosts (Lawton and Schroder 1977). In any event, morphological evidence indicates that a subtree of *Flexamia* evolved on *Muhlenbergia*. The first event (Fig. 66) appears to have been the divergence of the *serrata* and *decora* lineages. The *decora* subgroup is

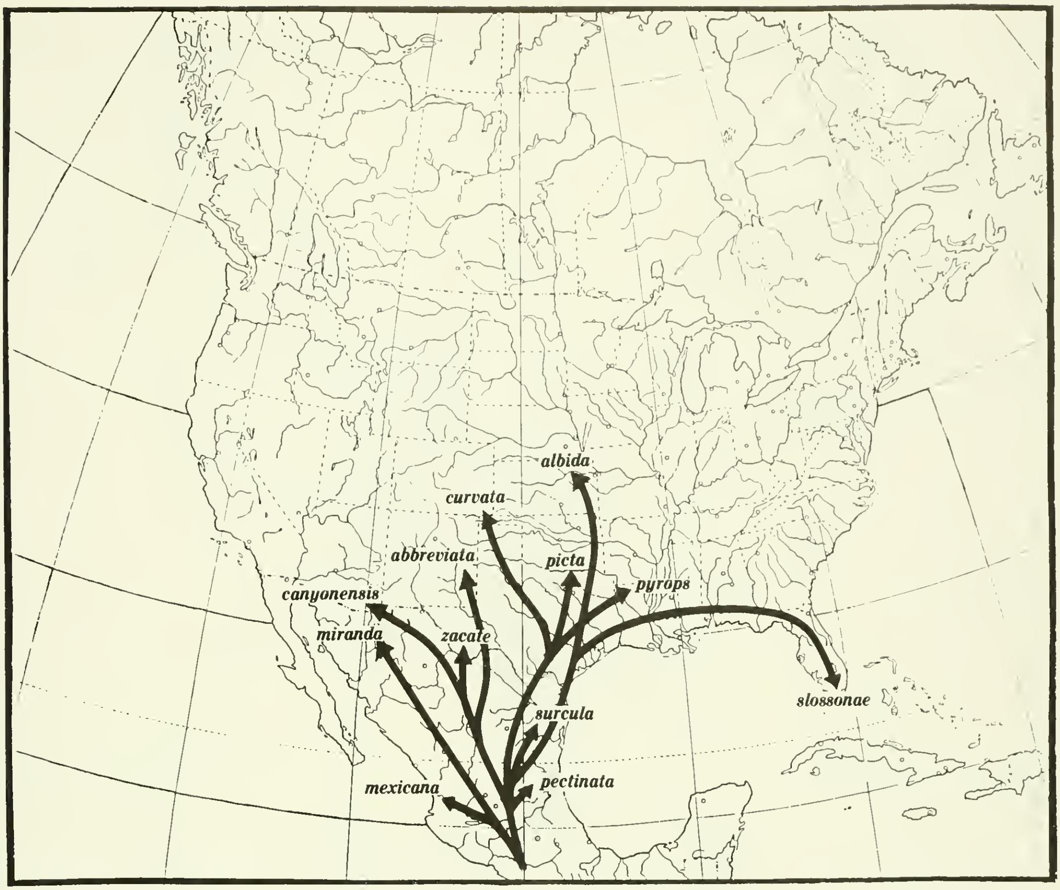


Fig. 64. Geographic interpretation of *Flexamia* phylogeny. Early evolution is postulated to be Mexican. The *Spartopyge* lineage diverged into *mexicana* and *miranda*. From this lineage *Flexamia* diverged. The first major node involved the divergence of the *pectinata* group, perhaps as a result of specialization on *Bouteloua curtipendula*. This divergence is hypothesized to have occurred in the grasslands of northeastern Mexico, a region thought to have remained stable over recent geologic history (Rosen 1978). Subsequent divergences, which occurred in the same general region of Mexico, were those of the *abbreviata-zacate* and *curvata-picta* lineages. The *abbreviata* lineage adapted to *Bouteloua* spp., the *curvata* group to *Buchloë dactyloides*, and the *picta* group to *Aristida* spp. The divergence of the *albida* lineage, characterized by a single, plesiomorphically ventral aedeagal process, may have occurred somewhat north of the Sierra Madre Orientale region, perhaps in Texan grasslands. Many contemporary species emerged from this lineage. The most plesiomorphic of these (members of the *albida* group) are relatively uncommon today; *albida* and *slossonae* do not appear to be strict host specialists, a feeding habit that we hypothesize to be plesiomorphic for the genus. Actual divergences in temperate zones may have occurred farther south than diagrammed, if they occurred during periods of glacial advance.

presumed to have divided by vicariance during glacial episodes into a Rocky Mountain-Canadian (*decora*) lineage, and a Great Basin lineage (*youngi*), both specialists on *M. richardsonis*. Alternatively, a second lineage developed, leading to a New Mexican montane lineage (*modica*) that transferred from *Muhlenbergia richardsonis* to *Muhlenbergia repens*. Further divergence led to *arenicola* (host: *Muhlenbergia pungens*) and to a set of sister species (*celata-stylata*) that specialized on *Muhlenbergia* or *Redfieldia* (and possibly other grasses of sandy grasslands), respectively. Finally, this line appears to have transferred from *Muhlenbergia* to the vast resource of *Bouteloua gracilis* in the plains region of New Mexico. This resource has been shared with *abbreviata*, which arrived in the New Mexican plains by an entirely different geographic route (i.e., Mexican mixed *Bouteloua*

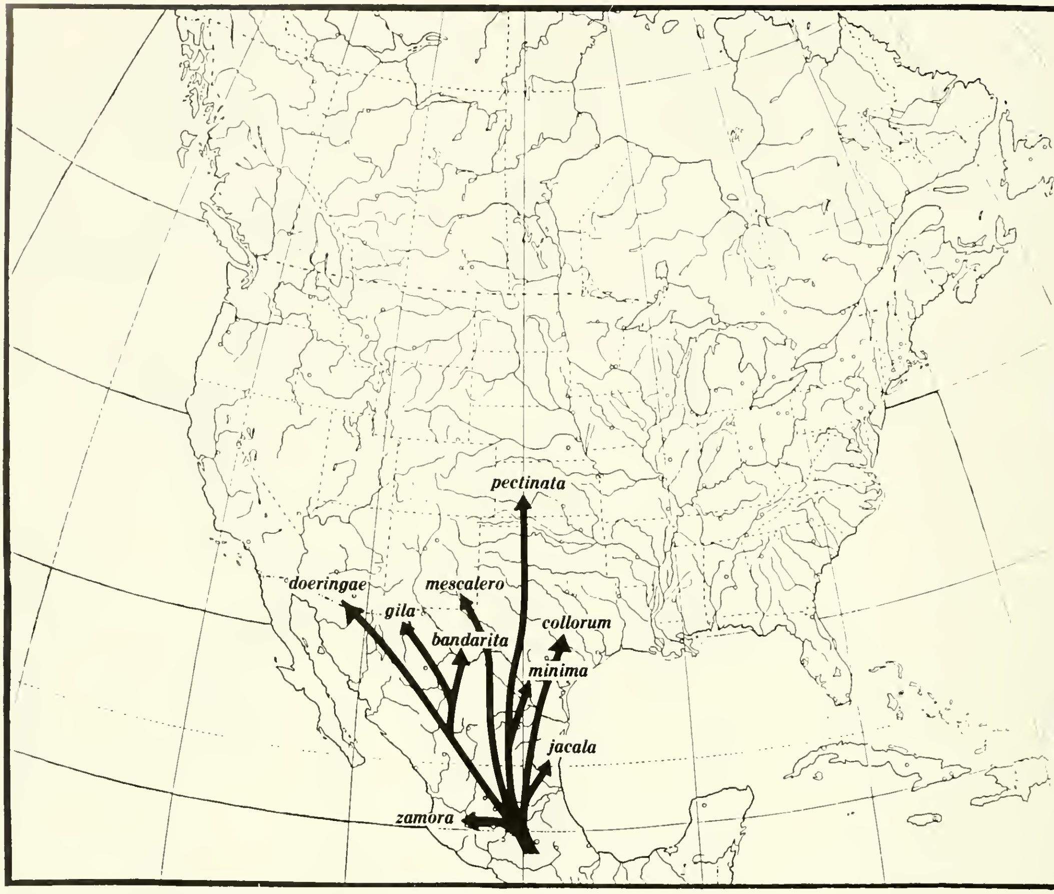


Fig. 65. Geographic interpretation of phylogeny of the *pectinata* group. A focal origin in grasslands of eastern Mexico is hypothesized. A western lineage comprised *gila*, *bandarita*, and *doeringae*. This lineage speciated exclusively on *Bouteloua curtipendula*. Morphological data suggest that *mescalero*, which apparently transferred to *Muhlenbergia pauciflora*, belongs on a deep branch. The subtree consisting of *zamora*, *minima*, and *pectinata* is closely related to the *doeringae* subtree; like all members of that subtree, *pectinata* specializes on *B. curtipendula* (side-oats grama). *F. collorum* may have been derived from a lineage on *B. curtipendula*, since its host is *B. uniflora*, which is closely related to side-oats grama. The host of *jacala* is unknown.

grasslands). (Interestingly, in contrast to *Athysanella* species [Hicks et al. 1988], both *Flexamia* blue grama specialists colonize this host throughout most of its range in New Mexico). A sister species, *arizonensis*, transferred to another dominant southwestern grass, *Aristida purpurea*. We emphasize that considerable climatic diversity exists today in the Southwest and no doubt has existed throughout the Pleistocene and Holocene as the result of elevational gradients (Axelrod and Raven 1985, Cole 1986, Cronquist 1978, Thompson and Mead 1982, VanDevender and Spaulding 1979). Therefore, evolutionary processes that might take place only over wide geographic distances in regions of relatively constant elevation may be focused in small geographic areas in the Southwest.

Another lineage, possibly more closely allied to the *ritana* than *serrata* lineage, presumably diverged in grasslands of the southern plains. This is the *inflata* subgroup of the *flexulosa* group. One contemporary representative (*inflata*) exhibits one of the widest host ranges in the genus; largest populations occur on *Muhlenbergia asperifolia* in wetland areas. If this apparent preference indicates an ancestral *Muhlenbergia* host, it would be necessary to postulate a monumental subsequent widening of host range to pooid grasses or

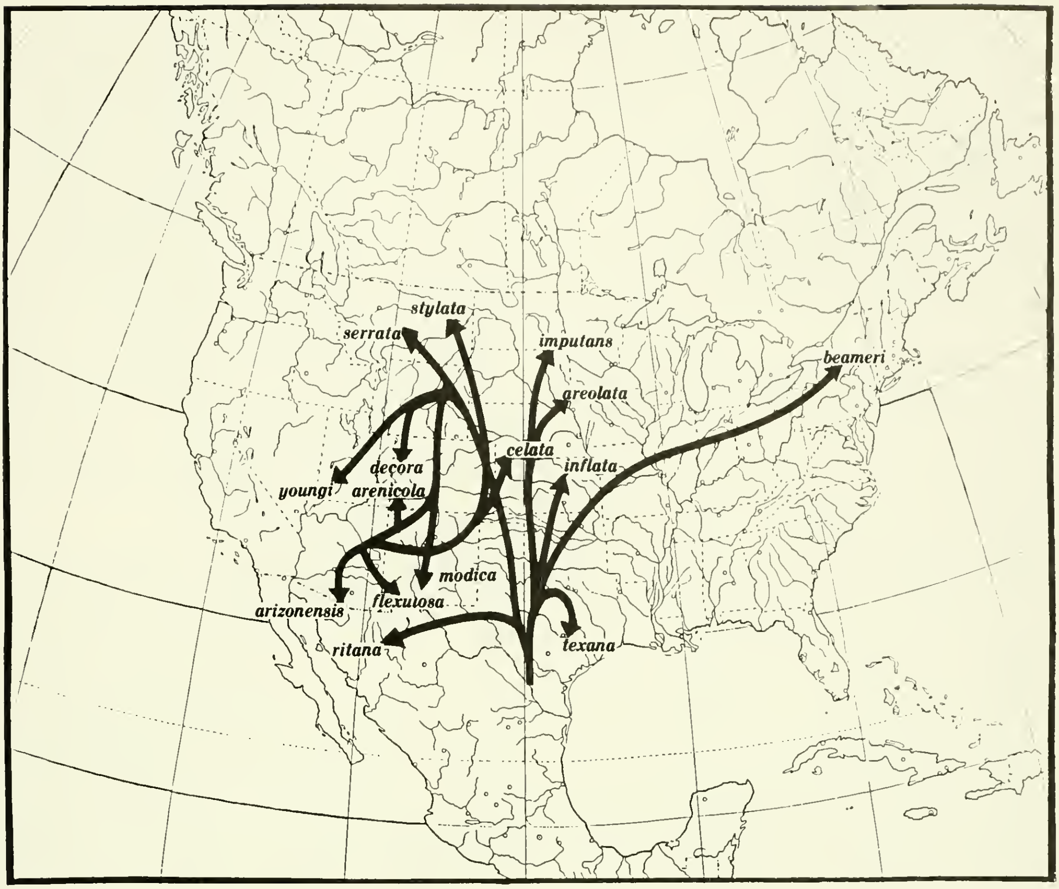


Fig. 66. Geographic interpretation of phylogeny of the *serrata*, *ritana*, *flexulosa*, *imputans*, and *areolata* groups. Texan grasslands may have been a focal area for initial divergence of lineages. *F. serrata* appears to be a *Muhlenbergia* specialist. The *ritana* group appears to have diverged in the Southwest. The contemporary distributions of the *albida*, *serrata*, and *ritana* groups suggest that they may have speciated by vicariant mechanisms or, in the case of *serrata*, by a combination of vicariance and host transfer. An eastern lineage consists of *inflata* and *beameri*. From a biogeographic perspective, it is most reasonable to propose an independent origin of *texana* and *beameri*, each from *inflata* or a closely related lineage. The present-day distribution of *inflata* suggests that it diverged in cool, temperate grasslands; Texas, of course, was cool during glacial maxima. In general, events postulated as northern in these reconstructions could have taken place much farther south during glaciations. The *imputans-areolata* lineage appears to have diverged in the prairie, on *Muhlenbergia cuspidata* and *Eragrostis spectabilis*, respectively. The western lineage of the *flexulosa* group may be related (see Fig. 59) to the *serrata* group; if this association can be confirmed, the derivation of the *decora* set of sister species from the *serrata* lineage would make an attractive hypothesis from a biogeographic standpoint, since all of the species (including *youngi*) specialize on *Muhlenbergia richardsonis*. Derivation of *modica* (host: *Muhlenbergia repens*) and *arenicola* (host: *Muhlenbergia pungens*) represents further evolution that occurred by host transfers within *Muhlenbergia*. The derivation of *flexulosa* and *arizonensis* by host transfer may have been a consequence of the regional abundance (in New Mexico and eastern Arizona) of their hosts, *Bouteloua gracilis* and *Aristida purpurea*, respectively; presumably, the region was colonized from the north. Finally, derivation of *celata* (host: *Redfieldia flexuosa* and perhaps other sandhill grasses) and *stylata* (hosts: *Muhlenbergia* spp.) is hypothesized to have followed a high-plains route around the eastern edge of the high Rocky Mountains.

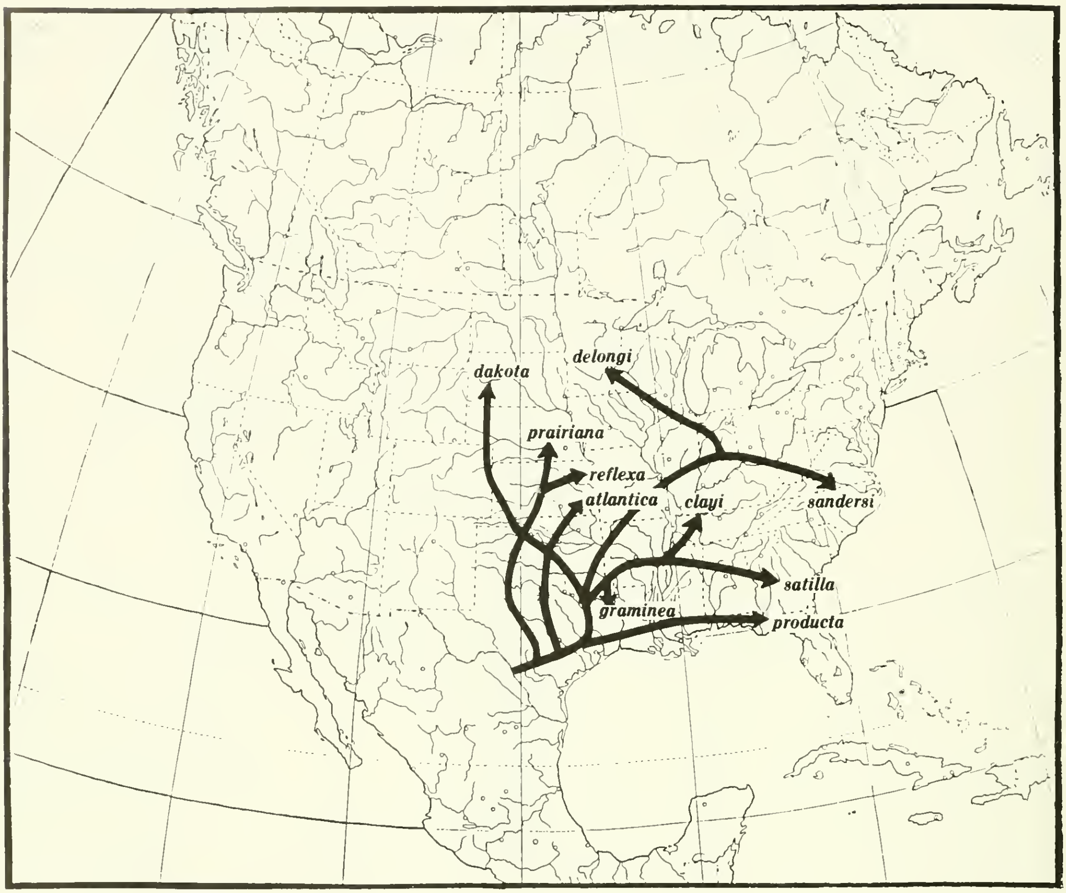


Fig. 67. Geographic interpretation of the phylogeny of the *prairiana* group. Although present-day distributions and host preferences do not offer obvious hypotheses for speciation mechanisms, an origin for the *prairiana* group in Texan grasslands is hypothesized. From this region *prairiana* presumably moved northward in postglacial episodes, where it adapted to little bluestem (*Schizachyrium scoparium*) or other andropogonoid grasses. In the tall-grass prairie, *reflexa* diverged from this lineage; this species often seems to be associated with big bluestem (*Andropogon gerardii*), particularly in glades of the eastern United States. *F. atlantica* may have transferred in postglacial times from chlorodoid grasses, on which it predominates in the Southwest, to switchgrass, *Panicum virgatum*. This host has been a conduit for colonization by *atlantica* of the eastern United States, including the Atlantic coastal prairies, where its host achieves high importance. Derivation of *sandersi* may have occurred by transfer to *Andropogon virginicus*, the first colonist in early fire succession in the Southeast. From this lineage, presumably post-Wisconsinan, *delongi* may have diverged by colonization of little bluestem in the glaciated area northwest of Illinois. Specialization on *Schizachyrium scoparium* and subsequent divergence led to *dakota* in the dry prairies of the plains, to *graminea* in Texas and northward through the tall-grass prairie, and to a lineage of eastern species. These species, also residents of andropogonoid grasses, are residents of the Gulf Coast (*satilla*), or the Appalachian mountains to Maine and cool, temperate savannas of Illinois and Ohio (*clayi*).

*Juncus*. It may be more likely that the currently observed host range breadth represents simply a retention of plesiomorphic generalism. In any event, this lineage has spawned two additional species: *texana* (south central Texas) and *beameri* (west slope of the Adirondack Mountains, New York). The circumstances surrounding these divergences are unclear, since we have no data on their host relationships.

After divergence of *inflata*, another lineage diverged in the prairie, leading to *imputans* (probable host: *Muhlenbergia cuspidata*) and *areolata* (host: *Eragrostis spectabilis*) on one hand, and to the *prairiana* group on the other.

All speciation events of the *prairiana* group (Fig. 67) occurred either in prairie, savanna, or southeastern grasslands. We hypothesize

an ancestor for this group that was adapted to both chloridoid and panicoid grasses. From such an ancestor, *prairiana* (host: *Schizachyrium* or *Bothriochloa*) and *reflexa* (host: *Andropogon gerardii*) were derived, as were *atlantica* (hosts: chloridoid grasses and/or *Panicum virgatum*), and *producta* (hosts: chloridoid grasses, or [possibly] a habitat specialist). Finally, specialization on *Schizachyrium scoparium* and/or *Andropogon virginicus* led (Fig. 67) to lineages that adapted to the most xeric of *Andropogon* habitats (*dakota*, a *Schizachyrium* specialist of the western Great Plains), *graminea* (a *Schizachyrium* specialist of the tall-grass prairie), and the *sandersi-delongi* and *satilla-clayi* sister pairs of eastern andropogonoid grasslands.

## Stages of Speciation

Mayr (1942) believed that at any given time all stages of evolution should be observable. We believe that this is indeed the case in the genus *Flexamia*. We recognize at least 10 levels in the process of speciation in *Flexamia:*

1. *Nonisolated ephemeral populations:* (i) Many populations of *Flexamia inflata* appear to be ephemeral. These populations often occur on pooid grasses such as *Poa* or *Festuca;* presence of immature insects confirms oviposition; (ii) *F. abbreviata* colonizes *Muhlenbergia richardsonis* in the Sacramento Mountains of New Mexico and *M. reverchonii* in the Edwards Plateau of Texas, although in the latter case we have not confirmed oviposition.

2. *Nonisolated stable populations:* (i) *F. inflata* consistently colonizes path rush (*Juncus tenuis*) in Illinois and Maryland; populations, including immatures, are found regularly on that host. This is an especially interesting case, since it may represent an interfamily transfer by a species that has limited oligophagy. (ii) *Flexamia atlantica* regularly colonizes large plantings of weeping love grass (*Eragrostis spectabilis*) and bermudagrass (*Cynodon dactylon*) in Oklahoma and Texas. (iii) Similarly, *producta* colonizes bermudagrass and *Zoysia japonica* in Maryland. These are essentially "natural experiments" that may mimic to a large degree, but in a shorter geologic time period, the effect of radical changes in the dominance hierarchy of grasses induced by cyclic climatic change.

3. *Disjunct populations that have not diverged morphologically:* In the following cases we have found no morphological variation associated with disjunct populations. (i) A disjunct population of *dakota*, a specialist on *Schizachyrium scoparium* in the western Great Plains, occurs on that host in the Loess Hills of western Iowa. (ii) *Flexamia reflexa* occurs (always, it seems, in association with big bluestem, *Andropogon gerardii*) in isolated grassland islands in the eastern deciduous forest as far east as the Soldier's Delight serpentine barrens in Baltimore County, Maryland.

4. *Isolated stable populations with minor morphological divergence:* In each of the following cases the populations may or may not represent biological species. (i) Two disjunct populations (Nebraska Sand Hills and Four Corners or Anasazi populations) of *arenicola* have been discovered; the unpaired, aedeagal processes of the Anasazi population always break, whereas the processes of the Sand Hills population rarely break. Other characters have not been found to separate these populations, each of which specializes on *Muhlenbergia pungens*. The host population is also separated into disjunct populations. (ii) The Mammoth Lakes population of *youngi*, probably isolated in eastern California in a region rich in endemics, has diverged somewhat from the population in the eastern Great Basin. (iii) Populations of *prairiana* on *Bothriochloa* in the Southwest have begun to diverge from the prairie *Schizachyrium* populations, perhaps as the result of phenological isolation. In this case divergence of female rather than male structures may signal the emergence of a new species.

5. *Recent (Holocene) speciations:* (i) The separation of *delongi* from the *sandersi* lineage may represent a postglacial transfer from *Andropogon virginicus* to *Schizachyrium scoparium* in the glaciated region of the northern prairie. (ii) The divergence of *clayi* and *satilla* may reflect phenological isolation between Gulf Coast and Appalachian populations.

6. *Pleistocene speciations:* Biological and biogeographic circumstances strongly suggest that *decora* and *youngi* represent vicariant populations of a common lineage that diverged during Pleistocene climatic cycles, retaining *Muhlenbergia richardsonis*.

7. *Vicariance and semiisolation:* In the case of Mexican and Southwestern grasslands, speciation was perhaps achieved by vicariance

during long periods of semiisolation. It is possible, in the case of certain species, that there may have been a punctuated infusion of genes into semiisolated populations as the climate became more mesic (Milstead 1960) and the distance between host stands of side-oats grama decreased. In any event the emergence of *gila*, *doeringae*, *bandarita*, *zamora*, *minima*, and *pectinata*, closely related species that appear to partion the range of side-oats grama, must have entailed different speciation mechanisms than those described above and are clearly enforced today by phenological isolation.

*8. Distinct species with obvious sisters:* We consider the sister pairs of *picta-pyrops*, *curvata-surcula*, *canyonensis-zacate*, and *prairiana-reflexa* to be obvious sisters that occur in ambiguous circumstances that suggest no particular age for their divergence. In some cases (*surcula-curvata* [tropical/temperate] and *zacate-canyonensis* [Chihuahuan/Sonoran]) the biogeographic circumstances for the divergences are clear.

*9. Species with distant sisters:* We consider the *albida-slossonae* sister pair to represent a historically remote divergence. *Flexamia slossonae* is a subtropical species that has many autapomorphies separating it from other *Flexamia* species. However, common characters of habitus and male genitalia leave no doubt that it is a sister to the tall-grass prairie species *albida*.

*10. Orphans:* The characteristics of *grammica* are sufficiently unique that it must be considered an orphan within the genus. In the absence of a contemporary link, the relationships to other extant species of the genus are obscure.

From the above examples we feel that our experience with *Flexamia* elegantly confirms Mayr's hypothesis.

## CONCLUSIONS

The initial choice of *Flexamia* as a model for the study of the role of host plants in insect evolution was a fortuitous one. Whereas some speciation events in *Flexamia* must have occurred by host transfer, others surely occurred by vicariance. Further, there is a tendency of individuals representing advanced lineages to be reduced in size and complexity, and to be more highly specialized in their host choice than their ancestors. There is therefore an immense stake in arriving at a well-substantiated phylogenetic hypothesis for the genus that is supported by independent lines of evidence. In particular, if advances in the study of molecular evolution prove to be adaptable to the study of small insects, we believe that *Flexamia* would provide an excellent model for study. Because the knowledge of *Flexamia* hosts is now adequate, obtaining live material of most species for such a study would be an achievable task. The rewards of further detailed studies would be many but would include, especially, important insights into the evolution of life-history strategies of sap-sucking insects.

When we began our studies of *Flexamia*, whose species number had remained relatively constant for a number of years, we did not dream that there were many remaining species awaiting discovery. It is difficult for us to guess, given the results reported here, how far we have fallen short, even now, of a complete inventory. Our discovery of the role of climate in inducing and reinforcing cicadellid speciation makes it clear that the biogeographically rich areas of the Southwest may well have many interesting stories that still await us.

In particular there may well be Mexican species awaiting discovery. For example, our phylogenetic hypothesis suggests that there may have been at one time a species with the plesiomorphic dorsal stripes of *Spartopyge*, *grammica*, and *albida*, but which possessed a full complement of four aedeagal processes. Because of the compelling logic of all phylogenetic schemes for its existence, such a species seems so real to us that we have jokingly referred to it as "ancestris." Is it possible that this species, or a closely related descendant of it, may actually exist in an unexplored Mexican grassland? It is questions such as these that have driven us to return repeatedly to the grasslands of the Southwest, which prove to be every bit as full of enigmas as they are of answers.

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There is a Japanese proverb that advises those who drink water from a well today to remember the ancestors who dug the well. The *Flexamia* well has been dug with many

spades. The early biological work of E. D. Ball, H. Osborn, D. M. DeLong, and R. H. Beamer is implicit in our work. H. H. Ross introduced us to the genus, framed many of the questions that we discuss, and left much unpublished material from his grasslands (GL) project. D. A. Young, whose 1958 monograph with B. P. Beirne continues to be an important tool for students of *Flexamia*, kindly permitted us to redraw many structures from drawings in his monograph. We are particularly pleased to acknowledge the advice and encouragement of P. W. Oman, given especially to the senior author during his early years at Beltsville. Further, a large fraction of USNM *Flexamia* had been collected and correctly determined by Oman; this material was extremely valuable in our study. Earlier studies on *Flexamia* at Beltsville were assisted by M. E. Coan, J. P. Kramer, and, in later years, J. E. Lowry, whose illustration of *serrata* is presented here as Figure 1. All other drawings were done by Debi Roney. Robert Almond and Edward Clark gave advice and assistance on the graphics. Host records were retrieved from a computerized index developed by D. E. Lynn. T. Mogel assisted with the scanning electron microscopy. Assistance with phylogenetic programs was provided by Mary Mickevich. We acknowledge further the assistance of G. W. Byers, P. S. Cwikla and C. P. Triplehorn, M. W. Nielson, and T. J. Henry and R. C. Froeschner, who made available the *Flexamia* collections of Kansas University, Ohio State University, Monte Bean Life Science Museum (Brigham Young University), and the United States National Museum, respectively. K. G. A. Hamilton made available the *Flexamia* material from the Canadian National Collection and provided a wealth of stimulating comments on the manuscript. M. Schauff made many useful comments on the manuscript. So many friends have helped in our field studies that all cannot be acknowledged. We are especially indebted, however, to Kelly Allred of New Mexico State University for continuing lessons on New Mexico agrostology. Charles T. Mason, Jr., assisted with grasses of Arizona. R. Chambers of the U.S. Soil Conservation Service drove us to the type locality of *collorum* and called our attention to the host. Mike Fleming of Big Bend National Park and Jim Walters of Guadalupe National Park assisted field studies there, and Barton Warnock identified many plant specimens from Big Bend National Park and the Davis Mountains. Riley Nelson of BYU provided collections from the Colorado Plateau. P. Cubbage assisted with fieldwork. Judith Leach, wife of the senior author, assisted during many field trips and also made valuable editorial comments on the manuscript. The editorial staff of *The Great Basin Naturalist* helped in many unusual ways to assure timely completion of the paper. Finally, H. D. Blocker suggested that the time for this paper had come, sorted more than 1,000 unidentified *Flexamia* from the KU cicadellid collection, provided *Flexamia* material and records from the KSU collection, read various drafts of the manuscript, and encouraged us in countless other ways. To all these workers, and many that remain unnamed, we offer our sincerest gratitude.

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# APPENDICES

## APPENDIX I. Specimens examined[1].

| Species | Holotype | Paratype(s) | BARC | CNC | KU | OSU | USNM |
|---|---|---|---|---|---|---|---|
| *minima* | OSU(h) | none | 0 | 0 | 0 | 1 | 8 |
| *zamora* | OSU(h) | OSU(p) | 0 | 0 | 0 | 9 | 0 |
| *pectinata* | USNM(c) | USNM(c) | 57 | 5 | 150 | 45 | 75 |
| *gila* | USNM(h) | p[2] | 9 | 0 | 0 | 0 | 0 |
| *bandarita* | USNM(h) | p[2] | 5 | 0 | 0 | 6 | 0 |
| *doeringae* | KU(h) | USNM(p) | 35 | 0 | 68 | 24 | 91 |
| *collorum* | USNM(h) | p[2] | 81 | 0 | 0 | 0 | 0 |
| *jacala* | USNM(h) | none | 0 | 0 | 0 | 0 | 1 |
| *mescalero* | USNM(h) | p[2] | 26 | 0 | 0 | 0 | 0 |
| *abbreviata* | USNM(c) | USNM(c) | 765 | 141 | 661 | 74 | 409 |
| *zacate* | USNM(h) | p[2] | 96 | 0 | 0 | 0 | 0 |
| *canyonensis* | USNM(h) | USNM(p) | 9 | 0 | 0 | 0 | 2 |
| *surcula* | OSU | OSU | 72 | 0 | 10 | 57 | 37 |
| *curvata* | OSU | OSU | 560 | 81 | 209 | 77 | 107 |
| *grammica* | USNM(l) | KU(p) | 47 | 64 | 164 | 48 | 109 |
| *picta* | OSU(h) | USNM(c) | 285 | 107 | 202 | 135 | 112 |
| *pyrops* | KU(l) | KU(c) | 56 | 39 | 56 | 83 | 162 |
| *albida* | USNM(c) | USNM(c) | 46 | 1 | 7 | 17 | 19 |
| *slossonae* | USNM(h) | none | 12 | 0 | 50 | 0 | 18 |
| *serrata* | KU(h) | KU(p) | 56 | 98 | 20 | 0 | 14 |
| *ritana* | KU(h) | USNM(p) | 0 | 0 | 17 | 0 | 5 |
| *arizonensis* | USNM | USNM(p) | 177 | 11 | 114 | 20 | 94 |
| *flexulosa* | USNM(l) | USNM(c) | 380 | 211 | 254 | 51 | 353 |
| *arenicola* | USNM(h) | USNM(p) | 91 | 0 | 0 | 0 | 5 |
| *celata* | USNM(h) | USNM(p) | 49 | 0 | 4 | 0 | 5 |
| *stylata* | USNM(l) | USNM(c) | 83 | 67 | 66 | 9 | 70 |
| *decora* | KU | USNM(p) | 95 | 246 | 177 | 3 | 28 |
| *youngi* | USNM | p[2] | 30 | 0 | 5 | 0 | 0 |
| *modica* | KU | USNM(p) | 377 | 0 | 110 | 3 | 8 |
| *inflata* | USNM(c) | USNM(c) | 665 | 103 | 257 | 146 | 155 |
| *beameri* | KU | USNM(p) | 0 | 0 | 7 | 0 | 0 |
| *texana* | USNM | USNM(p) | 0 | 0 | 0 | 0 | 10 |
| *imputans* | OSU(c) | OSU(c) | 4 | 0 | 10 | 11 | 19 |
| *areolata* | USNM(l) | USNM(c) | 37 | 51 | 42 | 51 | 88 |
| *prairiana* | OSU | OSU | 612 | 44 | 193 | 23 | 172 |
| *reflexa* | USNM | USNM(c) | 25 | 1 | 1 | 8 | 26 |
| *atlantica* | OSU | OSU(p) | 378 | 17 | 8 | 12 | 44 |
| *dakota* | USNM(h) | USNM(p) | 209 | 3 | 1 | 0 | 2 |
| *producta* | (BNM) | USNM(c[3]) | 4 | 5 | 136 | 117 | 267 |
| *sandersi* | OSU(h) | OSU(h[4]) | 45 | 3 | 60 | 31 | 126 |
| *delongi* | (INHS) | none | 0 | 26 | 1 | 39 | 13 |
| *graminea* | OSU(h) | none | 176 | 28 | 105 | 10 | 190 |
| *clayi* | USNM(h) | USNM(p) | 148 | 9 | 115 | 47 | 3 |
| *satilla* | CNC(h) | CNC(p) | 0 | 2 | 2 | 0 | 0 |

[1]Numbers reflect content of collection before redistribution at end of study. Type distribution occurred after this enumeration (c = cotype; h = holotype; l = lectotype; p = paratype). Parentheses = specimen not examined.

[2]See text for distribution of paratypes.

[3]Cotype of *visenda* (= *producta*).

[4]Holotype of *bidentata* (= *sandersi*).

APPENDIX II. PART I. Character matrix for PHYSYS.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| DISTIN | SIMPLE | ABSENTP | ? | SINUATC | THICK | 1 | ELONGA |
| SHORTL | TAPER | ABSNT | FLAREDG | APODNOX | APOPRIM | 2 | ELONGA |
| CONNAR | FORCEPY | PRIMPL | DEEPST | ABSTR | BRFACE | 3 | ELONGA |
| DISTIN | SIMPLE | ABSENTP | ? | LEFTC | THICK | 1 | MEXICAN |
| SHORTL | TAPER | ABSNT | APICALG | APODEXP | APOPRIM | 2 | MEXICAN |
| CONNAR | PRIMPY | PRIMPL | PARALST | PRESTR | CONBLF | 3 | MEXICAN |
| DISTIN | SIMPLE | ABSENTP | ? | LEFTC | THIN | 1 | MIRAND |
| SHORTL | TAPER | ABSNT | APICALG | APODEXP | APOPRIM | 2 | MIRAND |
| CONNAR | CNSTRPY | PRIMPL | EXCVST | PRESTR | CONBLF | 3 | MIRAND |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | MINIMA |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APOPARL | 2 | MINIMA |
| CONNAR | BULBPY | ACUTPL | TOOTHST | ABSTR | BRFACE | 3 | MINIMA |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | ZAMORA |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APOPARL | 2 | ZAMORA |
| CONNAR | BULBPY | LNGBRPL | OUTRST | ABSTR | BRFACE | 3 | ZAMORA |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | PECTIN |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APOPARL | 2 | PECTIN |
| CONNAR | BULBPY | RECTPL | TOOTHST | ABSTR | BRFACE | 3 | PECTIN |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | BANDAR |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APORECU | 2 | BANDAR |
| CONNAR | BULBPY | LNGBRPL | INNRST | ABSTR | BRFACE | 3 | BANDAR |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | GILA |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APORECU | 2 | GILA |
| CONNAR | BULBPY | LNGBRPL | INNRST | ABSTR | BRFACE | 3 | GILA |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | DOERIN |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APOPARL | 2 | DOERIN |
| CONNAR | BULBPY | RECTPL | PROCST | ABSTR | CONBLF | 3 | DOERIN |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | COLLOR |
| SHORTL | TAPER | ABSNT | FLAREDG | APODEXP | APORECU | 2 | COLLOR |
| CONNAR | BUDPY | SHORTPL | TOOTHST | ABSTR | BRFACE | 3 | COLLOR |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | JACALA |
| SHORTL | TAPER | ABSNT | FLAREDG | APODNOX | APORECU | 2 | JACALA |
| CONNAR | BULBPY | LNGBRPL | ? | ABSTR | BRFACE | 3 | JACALA |
| DISTIN | CAPITAT | ABSENTP | ? | LEFTC | THIN | 1 | MESCAL |
| SHORTL | TAPER | ABSNT | FLAREDG | APODNOX | APOCLOS | 2 | MESCAL |
| CONNAR | BULBPY | LNGROPL | DEEPST | ABSTR | BRFACE | 3 | MESCAL |
| DISTIN | SHORTPR | ABSENTP | ? | STRAIT | LESTHIC | 1 | ABBREV |
| LONGERL | UNTAPER | ABSNT | SLITG | APODEXP | APOPARL | 2 | ABBREV |
| CONNAR | PRODPY | LOBATPL | INCISST | ABSTR | BRFACE | 3 | ABBREV |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THICK | 1 | CANYON |
| SHORTL | TAPER | ABSNT | MIDLENG | APODNOX | APORECU | 2 | CANYON |
| CONNAR | PRODPY | LOBATPL | LONGST | ABSTR | BRFACE | 3 | CANYON |
| DISTIN | FLARED | ABSENTP | ? | LEFTC | THIN | 1 | ZACATE |
| SHORTL | TAPER | ABSNT | SLITG | APODNOX | APORECU | 2 | ZACATE |
| CONNAR | PRODPY | LOBATPL | PROJST | ABSTR | BRFACE | 3 | ZACATE |
| DISTIN | ASYMPR | ABSENTP | ? | LEFTC | THICK | 1 | GRAMMI |
| SHORTL | TAPER | SERRATE | BIPROVG | APODNOX | APOWING | 2 | GRAMMI |
| CONNAR | NARRPY | SQUATPL | ROUNDST | PRESTR | CONBLF | 3 | GRAMMI |
| DISTIN | LONGPR | SUBAPP | ? | STRAIT | LESTHIC | 1 | SURCUL |
| LONGERL | UNTAPER | ENTIRE | BIPROVG | APODNOX | APOFORK | 2 | SURCUL |
| CONWIDE | SHORTPY | SHORTPL | BOXST | ABSTR | BRFACE | 3 | SURCUL |
| DISTIN | LONGPR | DISTALP | ? | STRAIT | LESTHIC | 1 | CURVAT |
| LONGERL | UNTAPER | ENTIRE | BIPRSLG | APODEXP | APOFORK | 2 | CURVAT |
| CONNAR | SHORTPY | SHORTPL | WIDINST | ABSTR | BRFACE | 3 | CURVAT |
| INDIST | FLANGED | SUBAPP | ? | STRAIT | THIN | 1 | PICTA |
| LONGSTL | UNTAPER | SERRATE | SUBAPIG | APODNOX | APOFORK | 2 | PICTA |
| CONNAR | ANGLPY | TAPERPL | SERRST | ABSTR | CONBLF | 3 | PICTA |
| INDIST | FLANGED | APPOSP | ? | SINUATC | THIN | 1 | PYROPS |
| LONGSTL | UNTAPER | SERRATE | SUBAPIG | APODNOX | APOFORK | 2 | PYROPS |
| CONNAR | ANGLPY | REDUCPL | EXTHST | ABSTR | TOOTHF | 3 | PYROPS |

APPENDIX II. PART I continued.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| DISTIN | BIFURC | FUSEDP | SAGGITV | LESSC | THICK | 1 | ALBIDA |
| SHORTL | TAPER | SERRATE | SUBVNPG | APODEXP | APOCLUB | 2 | ALBIDA |
| CONWIDE | WIDEPY | TAPERPL | TTHEXST | PRESTR | CONBLF | 3 | ALBIDA |
| PARTLY | BIFURC | FUSEDP | SAGGITV | RIGHTC | THICK | 1 | SLOSSO |
| SHORTL | UNTAPER | ENTIRE | SYMSLTG | APODNOX | APOWING | 2 | SLOSSO |
| CONPAFU | UNDIFPY | ACUTPL | TRILBST | PRESTR | CONBLF | 3 | SLOSSO |
| DISTIN | BIFURC | FUSEDP | SAGGITV | STRAIT | THICK | 1 | SERRAT |
| SHORTL | UNTAPER | ENTIRE | SUBVNPG | APODEXP | APOCLUB | 2 | SERRAT |
| CONWIDE | IRREGPY | CLEAVPL | LOBEDST | ABSTR | CONBLF | 3 | SERRAT |
| DISTIN | LYRIFO | FUSEDP | SAGGITV | LESSC | THICK | 1 | RITANA |
| SHORTL | UNTAPER | ENTIRE | SUBVNPG | APODNOX | APOCLAW | 2 | RITANA |
| CONNAR | OVATEPY | TAPERPL | ANGLST | REDUSTR | CONBLF | 3 | RITANA |
| DISTIN | SYMMET | SHORTV | SAGGITV | LESSC | LESTHIC | 1 | ARENIC |
| LONGERL | UNTAPER | ENTIRE | SUBAPIG | APODNOX | APOAWAY | 2 | ARENIC |
| CONNAR | ROUNDPY | INCISPL | NOTCHST | ABSTR | CONBLF | 3 | ARENIC |
| DISTIN | SYMMET | SHORTV | SAGGITV | STRAIT | LESTHIC | 1 | CELATA |
| LONGERL | UNTAPER | ENTIRE | SUBAPIG | APODNOX | APOPARL | 2 | CELATA |
| CONWIDE | THSTYPY | INCISPL | NOTCHST | ABSTR | CONBLF | 3 | CELATA |
| DISTIN | ASYMME | TWISTV | DISPLCV | RIGHTC | LESTHIC | 1 | STYLAT |
| LONGERL | UNTAPER | ENTIRE | SUBAPIG | APODNOX | APOTHIC | 2 | STYLAT |
| CONBROD | STYLPY | SQUARPL | BINOTST | ABSTR | CONBLF | 3 | STYLAT |
| DISTIN | SYMMET | SHORTV | SAGGITV | STRAIT | LESTHIC | 1 | ARIZON |
| LONGERL | UNTAPER | ENTIRE | SUBAPIG | APODNOX | APOFORK | 2 | ARIZON |
| CONNAR | VNPRPY | MINUTPL | SQUARST | ABSTR | CONBLF | 3 | ARIZON |
| DISTIN | SYMMET | SHORTV | SAGGITV | LEFTC | LESTHIC | 1 | FLEXUL |
| LONGERL | UNTAPER | SERRATE | SUBAPIG | APODNOX | APOFORK | 2 | FLEXUL |
| CONNAR | CAUDPY | MINUTPL | MEDNST | ABSTR | CONBLF | 3 | FLEXUL |
| DISTIN | SYMMET | FUSEDP | SAGGITV | LEFTC | THICK | 1 | DECORA |
| SHORTL | TAPER | SERRATE | APPRG | APODNOX | APOAWAY | 2 | DECORA |
| CONBROD | LOBEDPY | INCISPL | BINOTST | ABSTR | CONBLF | 3 | DECORA |
| DISTIN | ASYMME | RECURVP | DISPLCV | LESSC | LESTHIC | 1 | YOUNGI |
| LONGERL | TAPER | SERRATE | APPRG | APODNOX | APOTHIC | 2 | YOUNGI |
| CONBROD | BROADPY | INCISPL | BINOTST | ABSTR | CONBLF | 3 | YOUNGI |
| DISTIN | ASYMME | DECURVP | DISPLCV | LEFTC | THICK | 1 | MODICA |
| SHORTL | TAPER | SERRATE | SUBAPIG | APODNOX | APOAWAY | 2 | MODICA |
| CONBROD | OVATEPY | DEEPL | NOTCHST | ABSTR | CONBLF | 3 | MODICA |
| DISTIN | ASYMME | DECURVP | DISPLCV | RIGHTC | THIN | 1 | INFLAT |
| LONGSTL | UNTAPER | ENTIRE | SUBAPIG | APODNOX | APOFORK | 2 | INFLAT |
| CONWIDE | BOATPY | TAPERPL | BINOTST | ABSTR | CONBRF | 3 | INFLAT |
| DISTIN | TWISTED | RECURVP | DISPLCV | RIGHTC | THIN | 1 | BEAMER |
| LONGSTL | UNTAPER | ENTIRE | APPRG | APODNOX | APOTHIC | 2 | BEAMER |
| CONBROD | SHIPPY | SHORTPL | BINOTST | ABSTR | CONBRF | 3 | BEAMER |
| DISTIN | TWISTED | TWISTV | DISPLCV | STRAIT | THIN | 1 | TEXANA |
| LONGSTL | UNTAPER | ENTIRE | APPRG | APODNOX | APOREDU | 2 | TEXANA |
| CONWIDE | SHIPPY | SHORTPL | BINOTST | ABSTR | CONBRF | 3 | TEXANA |
| DISTIN | TWISTED | ? | LATERLV | STRAIT | THIN | 1 | IMPUTA |
| LONGSTL | UNTAPER | SERRATE | LATSLTG | APODNOX | APOHOOK | 2 | IMPUTA |
| CONWIDE | LGOVPY | TAPERPL | LOBEDST | ABSTR | BLFACE | 3 | IMPUTA |
| FUSED | TWISTED | ? | LATERLV | LEFTC | LESTHIC | 1 | AREOLA |
| LONGERL | UNTAPER | SERRATE | LATSLTG | APODNOX | APOAWAY | 2 | AREOLA |
| CONWIDE | BIZARPY | TAPERPL | PROCST | ABSTR | BLFACE | 3 | AREOLA |
| BARELY | INVERT | ? | DORSALV | STRAIT | LESTHIC | 1 | PRAIRI |
| LONGERL | UNTAPER | SERRATE | DORSALG | APODNOX | APOPEN | 2 | PRAIRI |
| CONFUSE | ELLIPY | NARRPL | NAROWST | ABSTR | VARCONF | 3 | PRAIRI |
| FUSED | INVERT | ? | BASFUSV | STRAIT | LESTHIC | 1 | REFLEX |
| LONGERL | UNTAPER | SERRATE | PROFUSG | APODNOX | APOCLOS | 2 | REFLEX |
| CONFUSE | UPTNPY | NARRPL | NAROWST | ABSTR | VARCONF | 3 | REFLEX |
| FUSED | WINDSW | ? | FUSEDV | STRAIT | LESTHIC | 1 | ATLANT |
| LONGERL | UNTAPER | SERRATE | LATG | APODNOX | APOWIDE | 2 | ATLANT |
| CONFUSE | THINPY | NOTCHPL | NAROWST | ABSTR | VARCONF | 3 | ATLANT |

APPENDIX II. PART I continued.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| FUSED | INVTWO | ? | TINYV | STRAIT | THICK | 1 | PRODUC |
| FUSEDL | UNTAPER | SERRATE | FUSEDG | APODNOX | APOPARL | 2 | PRODUC |
| CONFUSE | VNTLBPY | BOTTLPL | NAROWST | ABSTR | VARCONF | 3 | PRODUC |
| FUSED | INVTWO | ? | FUSEDV | STRAIT | THICK | 1 | DAKOTA |
| FUSEDL | UNTAPER | SERRATE | DORFUSG | APODNOX | APOCLOS | 2 | DAKOTA |
| CONFUSE | POSTPY | BOTTLPL | NAROWST | ABSTR | BRFACE | 3 | DAKOTA |
| FUSED | FUSPR | ? | REDUCV | STRAIT | THICK | 1 | SANDER |
| FUSEDL | UNTAPER | SERRATE | APPRSDG | APODNOX | APOWIDE | 2 | SANDER |
| CONFUSE | HIGHPY | NOTCHPL | NAROWST | ABSTR | BRFACE | 3 | SANDER |
| FUSED | FUSPR | ? | REDUCV | STRAIT | THICK | 1 | DELONG |
| FUSEDL | UNTAPER | SERRATE | APPRSDG | APODNOX | APOWIDE | 2 | DELONG |
| CONFUSE | HIGHPY | NOTCHPL | NAROWST | ABSTR | BRFACE | 3 | DELONG |
| FUSED | ASKEW | ? | FUSEDV | STRAIT | THICK | 1 | GRAMIN |
| FUSEDL | SPIRALT | SERRATE | SPIRALG | APODNOX | APOPARL | 2 | GRAMIN |
| CONFUSE | THICKPY | RECURPL | NAROWST | ABSTR | BRFACE | 3 | GRAMIN |
| FUSED | ASKEW | ? | FUSEDV | LEFTC | THICK | 1 | CLAYI |
| FUSEDL | SPIRALT | SERRATE | WIDSPIG | APODNOX | APOCLOS | 2 | CLAYI |
| CONFUSE | UPLOBPY | RECURPL | NAROWST | ABSTR | BRFACE | 3 | CLAYI |
| FUSED | ASKEW | ? | FUSEDV | LEFTC | THICK | 1 | SATILL |
| FUSEDL | SPIRALT | SERRATE | WIDSPIG | APODNOX | APOCLOS | 2 | SATILL |
| CONFUSE | UPLOBPY | RECURPL | NAROWST | ABSTR | BRFACE | 3 | SATILL |

APPENDIX II. PART II. Hypothesized character transformation in *Flexamia*. Data for PHYSYS.

| | | |
|---|---|---|
| AEDCONN;DISTIN-INDIST-PARTLY-BARELY-FUSED; | 1 | AEDCONN |
| AEDAPEX;SIMPLE-FLARED-CAPITAT,SHORTPR-[LONGPR-FLANGED, | 1 | AEDAPEX |
| BIFURC,LYRIFO,SYMMET-ASYMME-TWISTED-[INVERT-WINDSW, | 2 | AEDAPEX |
| [FUSPR-ASKEW],INVTWO]]; | 3 | AEDAPEX |
| ANTEPR;ABSENTP-SUBAPP-DISTALP-APPOSP-[FUSEDP-DECURVP, | 1 | ANTEPRO |
| RECURVP,[LONGV-SHORTV-TWISTV]]; | 2 | ANTEPRO |
| VENTRALP;SAGGITV-DISPLCV-LATERLV-DORSALV-BASFUSV-REDUCV | 1 | VENTRLP |
| TINYV-FUSEDV; | 2 | VENTRLP |
| AEDCURV;LEFTC-LESSC-STRAIT-SINUATC-RIGHTC; | 1 | AEDCURV |
| AEDTHIC;THICK-LESTHIC-THIN; | 1 | AEDTHIC |
| AEDLENG;SHORTL-LONGERL-LONGSTL-FUSEDL; | 1 | AEDLENG |
| AEDTAPER;TAPER-UNTAPER-SPIRALT; | 1 | AEDTAPER |
| AEDPRMG;ENTIRE-SERRATE; | 1 | AEDPRMG |
| GONOLOC;APICALG-FLARED-[SLITG-MIDLENG],[BIPROVG-[SUBVNPG- | 1 | GONOLOC |
| SYMSLTG],BIPRSLG,[SUBAPIG-APPRG,LATSLTG-DORSALG-[PROFUSG- | 2 | GONOLOC |
| [APPRSDG-SPIRALG-WIDSPIG],[FUSEDG-DORFUSG],LATG]]]; | 3 | GONOLOC |
| APOAPEX;APODEXP-APODNOX; | 1 | APOAPEX |
| APOARM;APOPRIM-[APOPARL-[APOCLAW-APOHOOK-APOPEN-APOCLOS- | 1 | APOARM |
| APOWIDE],[APOAWAY-APOTHIC-APOREDU],APOFORK,[APOCLUB- | 2 | APOARM |
| APOWING],APORECU]; | 3 | APOARM |
| CONKEEL;CONNAR-CONWIDE-CONBROD-CONPAFU-CONFUSE; | 1 | CONKEEL |
| PYGMAL;PRIMPY-FORCEPY-[CNSTRPY-[NARRPY-IRREGPY-WIDEPY- | 1 | PYGMAL |
| UNDIFPY],[BULBPY-BUDPY,PRODPY,[SHORTPY-ANGLPY,[OVATEPY- | 2 | PYGMAL |
| [LOBEDPY-[BOATPY-SHIPPY],BROADPY],[ROUNDPY-[VNPRPY-CAUDPY], | 3 | PYGMAL |
| [STYLPY-THSTPY]],[LGOVPY-BIZARPY,[ELLIPY-VNTLBPY,[UPTNPY- | 4 | PYGMAL |
| POSTPY,THINPY,[HIGHPY-UPLOBPY-THICKPY]]]]]]]; | 5 | PYGMAL |
| PLATES;PRIMPL-[LNGBRPL-RECTPL,SHORTPL],SQUATPL,[LNGROPL- | 1 | PLATES |
| LOBATPL-REDUCPL],[TAPERPL-[NARRPL-BOTTLPL-NOTCHPL-RECURPL], | 2 | PLATES |
| ACUTPL,[CLEAVPL-[INCISPL-SQUARPL,[DEEPL-MINUTPL]]]]; | 3 | PLATES |
| STERNUM;PARALST-EXCVST-ROUNDST,[TOOTHST-[OUTRST-DEEPST], | 1 | STERNUM |
| [INNRST-PROCST],[INCISST-LONGST-PROJST],[BOXST-WIDINST, | 2 | STERNUM |
| [SERRST-EXTHST]]],[TTHEXST-TRILBST,LOBEDST-[ANGLST- | 3 | STERNUM |
| [NOTCHST-BINOTST],[PROCST-NAROWST],[SQUARST-MEDNST]]]; | 4 | STERNUM |
| DORSVIT;PRESTR-REDUSTR-ABSTR; | 1 | DORSVIT |
| FACE;CONBLF-TOOTHF,[CONBRF-BRFACE],[VARCONF-BLFACE]; | 1 | FACE |

## APPENDIX II. PART III.

### Character Codes of *Flexamia* Species: Code Identification*

P = plesiomorphic; A = apomorphic

1. AEDCONN: Articulation (P) or fusion (A) of aedeagus and connective: DISTIN (P) (Figs. 6A,B,C,E); INDIST (Fig. 6D); BARELY (Fig. 6F); PARTLY (Y&B Fig. 9B) FUSED (Fig. 6G).

2. AEDAPEX: Morphology of aedeagal apex which may be simple, without processes or special structures (P), or with paired processes (A): SIMPLE (P) (Figs. 55C,F); FLARED (Figs. 12A–H); CAPITAT (Figs. 12I,22); SHORTPR (Fig. 7H); ASYMPR (Fig. 7E); LONGPR (Figs. 7F,G); FLANGED (Figs. 7K,L); BIFURC (Figs. 7A–C); LYRIFO (Fig. 7D); SYMMET (Figs. 31G,K); ASYMME (Figs. 31E,H,M); TWISTED (Fig. 31A); INVERT (Figs. 44D,G); WINDSW (Fig. 44A); INVTWO (Fig. 44I); FUSPR (Fig. 44B); ASKEW (Figs. 44F,H).

3. ANTEPR: Anteapical processes, which are absent (P), present as paired processes, or fused (A) into a single process: ABSENTP (Figs. 55C,F); SUBAPP (Fig. 7G); DISTALP (Fig. 7F); APPOSP (Fig. 7L); FUSEDP (Figs. 7A–D); LONGV (Fig. 31G); RECURVP (Fig. 38A); DECURVP (Fig. 31E); SHORTV (Figs. 31I–L); TWISTV (Fig. 31A).

4. VENTRLP: Phyletic twisting of the unpaired ventral process (see 3. ANTEPR), which was (P) symmetrically situated on the ventral surface of the aedeagus, but moved to the dorsum, and was (A) ultimately lost (Fig. 61), presumably by fusion: SAGGITV (Fig. 61A); DISPLCV (Fig. 61B); LATERLV (Fig. 61C); DORSALV (Fig. 61D); BASFUSV (Fig. 61E); REDUCV (Fig. 61F); TINYV (Fig. 61G); FUSEDV (Fig. 61H).

5. AEDCURV: Curvature (lateral aspect) of the aedeagus, which may be curved sinistrad (P), without curvature, sinuate, or curved dextrad (A): LEFTC (Figs. 7I,J); LESSC (Y&B Figs. 10B,11A); STRAIT (Fig. 7H); SINUATC (Y&B Fig. 2B); RIGHTC (Fig. 40A).

6. AEDTHIC: Thickness (lateral aspect) of the aedeagus, which may be thick (P), less thick, or thin (A); THICK (Fig. 7J); LESTHICK (Fig. 38A); THIN (Figs. 16A, 17A, 18A).

7. AEDLENG: Length of the aedeagus, which may be short (P), longer, even longer, or, finally (A), fused with the connective: SHORTL (Figs. 16A,7I,J); LONGERL (Fig. 6B); LONGSTL (Fig. 6D); FUSEDL (Fig. 6G).

8. AEDTAPR: Form of the aedeagal shaft which may be tapered (P), untapered, or, ultimately (A), tapered in association with a spiral gonopore: TAPER (Figs. 7I,J); UNTAPER (Fig. 7H); SPIRALT (Fig. 6G).

9. AEDPRMG: Form of the margins of the paired, apical, aedeagal processes which, if present, may have entire (P) or serrate margins (A): ABSNT (absent); ENTIRE (Figs. 7F,G); SERRATE (Figs. 44B–D).

10. GONOLOC: Form and position of the gonopore. In the plesiomorphic condition, this structure was apical and subcircular or ovate. In early stages in transformation the gonopore was subapical on the ventral surface. In the *flexulosa* group the gonopore may have reversed its distad movement from the aedeagal apex and returned to the apex, or nearly so; but in *imputans* and *areolata* the gonopore became associated with the unpaired process, which had moved to a lateral position on the aedeagal shaft. In *prairiana* the gradual twisting (see 4. VENTRLP) of the processes had stabilized with the gonopore in a dorsal, anteapical position. Transformation from this condition involved association with the unpaired process and movement with the process as it became appressed to the aedeagal shaft and, eventually, fused with the shaft. Ultimately, the fusion led to an elongate structure that winds around the shaft in a helical configuration: APICALG (Y&B Fig. 32B); FLAREDG (Figs. 12A–H); SLITG (Fig. 7H); MIDLENG (Fig. 6C); BIPROVG (Fig. 7G); SUBVNPG (Fig. 7B); SYMSLTG (Fig. 7C); BIPRSLG (Fig. 7F); SUBAPIG (Figs. 31E,J,M); APPRG (Fig. 31A); LATSLTG (Fig. 61C) DORSALG (Fig. 44G) PROFUSG (Fig. 44D); APPRSDG (Fig. 44B) SPIRALG (Fig. 44F); WIDSPIG (Figs 44H,J); FUSEDG (Fig. 44E); DORFUSG (Fig. 44I); LATG (Fig. 44A).

11. APOAPEX: Apices of the apodema arms may be expanded (P) or not expanded (A): APODEXP (Fig. 6B); APODNOX (Figs 6A,D,E).

*Characters are illustrated herein, in Young and Beirne (1958) (Y&B); Lowry and Blocker (1987) (L&B); or Hamilton and Ross (1975) (H&R).

12. APOARM: In dorsal aspect the apodemal arms in the plesiomorphic condition were parallel to the aedeagal shaft. Transformations from this state (A) involved several lines of development, some of which involved reduction of the arms, or direction of the apices toward or away from the sagittal plane: APOPRIM (Y&B Fig. 32B); APOPARL (Fig. 6B); APOCLAW (Y&B Fig. 11B); APOHOOK (Y&B Fig. 21B); APOPEN (Fig. 6F); APOCLOS (Y&B Fig. 28C); APOWIDE (R&C Fig. 2); APOAWAY (Y&B Fig. 14B); APOTHIC (Fig. 40B); APOREDU (Y&B Fig. 16B); APOFORK (Figs. 6A,D,E); APOCLUB (Fig. 8B); APOWING (Y&B Fig. 27B); APORECU (Figs. 6C, 16B, 17B, 19B, 20B).

13. CONKEEL: In lateral aspect the dorsal keels of the connective may be narrow (P), widened, or very much widened. Alternatively (A), the connective fused with the aedeagus, a process that resulted in the loss of an independent identity for the keels: CONNAR (Figs. 16A, 17A, 18A); CONWIDE (Y&B Fig. 12A); CONBROD (Fig. 40A); CONPAFU (Y&B Fig. 9B); CONFUSE (Fig. 6G).

14. PYGMAL: The male pygofer, plesiomorphically, was apparently undifferentiated. From this state a defined posterior lobe differentiated, as in *Spartopyge miranda*. Several lines of development (A) are postulated (Fig. 62): PRIMPY (Fig. 62S); FORCEPY (Fig. 55G); UNDIFPY (Fig. 62T); CNSTRPY (Fig. 62N); BULBPY (Figs. 62C-G); BUDPY (Fig. 62A); PRODPY (Figs. 62H,I); NARRPY (Fig. 62O); IRREGPY (Fig. 62P); SHORTPY (Figs. 62K,L); ANGLPY (Fig. 62M); WIDEPY (Fig. 62Q); OVATEPY (Fig. 62U); ROUNDPY (Fig. 62LL); STYLPY (Fig. 62OO); THSTYPY (Fig. 62PP); LOBEDPY (Fig. 62FF); BROADPY (Fig. 62KK); BOATPY (Fig. 62GG); SHIPPY (Figs. 62HH,II); LGOVPY (Fig. 62V); BIZARPY (Fig. 62Z); ELLIPY (Fig. 62W); VNTLBPY (Fig. 62AA); UPTNPY (Fig. 62X); POSTPY (Fig. 62BB) THINPY (Fig. 62Y); HIGHPY (Fig. 62CC); UPLOBPY (Fig. 62DD); THICKPY (Fig. 62EE) CAUDPY (Fig. 62NN); VNPRPY (Fig. 62MM)..

15. PLATES: The male plates, plesiomorphically, were apparently long and relatively wide. The broad aspect of the plates was retained in the *pectinata* group, but in subsequent lineages tended to be modified to become tapered. In the *flexulosa* group the tapered plates became notched to accommodate dorsally produced pygofers; in *arizonensis* and *flexulosa* this tendency is maximized. In the *prairiana* group the tapered design was modified by narrowing of the apical third of the plates, by the development of small apical notches, and by the plates ultimately becoming recurved: PRIMPL (Fig. 54C); SQUATPL (Fig. 8F); LNGROPL (Fig. 11I); LNGBRPL (Fig. 11B); RECTPL (Figs. 11C,F); SHORTPL (Fig. 11G); LOBATPL (Fig. 8E); REDUCPL (Fig. 9B); TAPERPL (Fig. 8A); NARRPL (Fig. 45A); BOTTLPL (Fig. 45E); NOTCHPL (Fig. 45C); RECURPL (Fig. 45H); ACUTPL (Fig. 8B); CLEAVPL (Fig. 8C); MINUTPL (Figs. 33A,B); INCISPL (Figs. 33C,D,E); SQUARPL (Fig. 34E); DEEPL (Fig. 33F).

16. STERNUM: The sternum VII was apparently plesiomorphically excavated. From this condition several lines of development (A) ensued. Many of these lines involved two pairs of teeth separated by an incision on the posterior margin of the sternum. In the *pectinata* group the development of the inner or outer sets of teeth relative to one another is an important character in species discrimination. In the *flexulosa* and *prairiana* groups, at a time that aedeagal evolution was proceeding rapidly, the sternum VII became a relatively stable apomorphy that underwent minimal transformation: PARALST (Y&B Fig. 32E); EXCVST (Y&B Fig. 33F); ROUNDST (Fig. 10F); TOOTHST (Figs. 14A,C,G); OUTRST (Fig. 14B); DEEPST (Fig. 14H); INNRST (Figs. 14D,E); PROCST (Fig. 14F); INCISST (Fig. 10E); LONGST (Fig. 10I); PROJST (Fig. 10L); BOXST (Fig. 10J); WIDINST (Fig. 10K); SERRST (Fig. 10G); EXTHST (Fig. 10H); TTHEXST (Fig. 10A); TRILBST (Fig. 10B); LOBEDST (Fig. 10C); ANGLST (Fig. 10D); NOTCHST (L&B Figs. 1F, 2F); BINOTST (Fig. 10R); PROCST (Fig. 10Q); NAROWST (Fig. 10S); SQUARST (Y&B Fig. 17F); MEDNST (Fig. 10M).

17. DORSVIT: Species of the genus *Spartopyge* possess conspicuous dorsal stripes (P) that appear to be homologous with the stripes in *albida*, *slossonae*, *ritana*, and *grammica*. The loss of stripes (A) is presumed to be homoplastic: PRESTR (Figs. 2A–C, 54A); REDUSTR (Fig. 2D); ABSTR (Figs. 2E,F).

18. FACE: The plesiomorphic face of *Flexamia* (and its ancestor *Spartopyge*) is presumed to be pale, with a conspicuously contrasting, black interocular band. In later lineages this habitus aspect was modified, as the interocular band became brown rather than black, as the distinction between the line and the remainder of the face became blurred, and, finally (A), as the face became essentially brown. In some transitional species, such as *prairiana*, the face varies widely from pale with a contrasting, brown interocular line to brown to (occasionally) nearly entirely black. We presume that loss of the plesiomorphic face condition, as with dorsal stripes, probably occurred in several lines: CONBLF (Figs. 3A,B,E,F,G); TOOTHF (*pyrops:* see text); BRFACE (Fig. 3H); CONBRF (contrasting brown face) VARCONF (variable contrast); BLFACE (Fig. 3C).

## APPENDIX III

### NOTES

PLANT NAMES.—*Andropogon gerardii* Vitman, big bluestem; *Andropogon virginicus* L., broomsedge; *Aristida dichotoma* Michx. var. *curtisii* Gray; *Aristida purpurea* Nutt.; *Bouteloua curtipendula* (Michx.) Torr., sideoats grama; *Bouteloua eriopoda* (Torr.) Torr., black grama; *Bouteloua gracilis* (Willd. ex H. B. K.) Lag. ex Griffiths, blue grama; *Bouteloua hirsuta* Lag., hairy grama; *Bouteloua pectinata* Featherley, tall grama; *Bouteloua uniflora* Vasey, Nealley grama; *Buchloë dactyloides* (Nutt.) Engelm., buffalograss; *Calamovilfa gigantea* (Nutt). Scribn. & Merr., big sandreed; *Calamovilfa longifolia* (Hook.) Scribner., prairie sandreed; *Cynodon dactylon* (L.) Pers., bermudagrass; *Distichlis spicata* (L.) Greene, salt grass; *Eragrostis curvula* (Schrad.) Nees, weeping lovegrass; *Eragrostis pectinacea* (Michx.) Nees, tufted lovegrass; *Eragrostis spectabilis* (Pursh) Steud., purple lovegrass; *Juncus tenuis* Willd., poverty rush; *Leptoloma cognatum* (Shult) Chase, fall witchgrass; *Muhlenbergia asperifolia* (Nees & Mey.) Paradi, scratchgrass; *Muhlenbergia cuspidata* (Torr. in Hook.) Rydb., plains muhly; *Muhlenbergia pauciflora* Buckley, New Mexican muhly; *Muhlenbergia porteri* Scribn. ex Beal, bush muhly; *Muhlenbergia pungens* Thurb., sand muhly; *Muhlenbergia repens* (Presl.) A. S. Hitchc., creeping muhly; *Muhlenbergia reverchonii* Vasey & Scribn., seep muhly; *Panicum capillare* L., witchgrass; *Panicum virgatum* L., switchgrass; *Poa pratensis* L., Kentucky bluegrass; *Redfieldia flexuosa* (Thurb.) Vasey, sand blowout grass; *Schizachyrium scoparium* (Michx.) Nash, little bluestem; *Sporobolus virginicus* (L.) Kunth., seashore dropseed; *Zoysia japonica* Steudl., zoysia grass.

PLANT RANGES.—Plant ranges were mapped using published range maps (Pohl 1968; Hitchcock 1971; McGregor 1977; Stubbendieck et al. 1986) and/or various floras (Gould 1975; Harrington 1954; Jepson 1925; Johnston 1943, 1963; Kearny and Peebles 1960; Küchler 1964; Lesueur 1945; Lonard and Judd 1980; Muller 1947; Rzedowski 1966, 1973, 1975, 1983); Shreve 1939, 1942; Steyermark 1963; Pohl 1966; and Welsh et al. 1987).

INSECT RANGES.—Occurrence of specimens was mapped on maps of the United States or North America (Goode Base Map, Department of Geography, University of Chicago, was used as a base). Specimens examined from the collections listed below were mapped. Canadian and Mexican records are mapped by locality; U.S. records were mapped by county to avoid extensive overlap of symbols. Some records from the collections of the Illinois State Natural History Survey (as reported in DeLong 1948), and the Kansas State University Collection were also mapped.

OTHER RECORDS.—Not all "records" were mapped. We refrained from mapping specimens that in our judgment represented possible or probable errors. These records included the following record for *clayi:* "Colfax, Cal., 8-7-30," from the OSU collection. Since *clayi* is a common Ohio species, but apparently does not occur west of the Mississippi River, this record is probably in error. Three records for *picta* seem questionable. Perhaps "Coronado N.F., Pena Blanca Resort, Arizona, 19 Aug. 1970, Harris and Harris, GL2019" (CNC) is valid. However, "Panama City, C. Z., July 23, 1920" (OSU), and "Mina, Mineral Co. Nevada, Aug. 20, 1955, GL274, Galloway" (CNC) seem less likely to be correct. For other unusual records, see discussion under *decora*, *areolata*, and *graminea*.

In all studies, some specimens (usually females) remain unidentified at the end of the study. One record of this kind is intriguing. The label "Cowan, Manitoba, 8 Aug., 1946, R. H. Beamer" (KU) is affixed to a single female that we cannot name. See field notes (later in this appendix) concerning this record.

COLLECTIONS UTILIZED.—We examined the *Flexamia* collections of the United States National Museum (USNM), Ohio State University (OSU), University of Kansas (KU), and the Canadian National Collection (CNC). Our own collection (Beltsville Agricultural Research Center [BARC]) contains, in addition to mounted specimens, a large inventory of unmounted but accessioned (Lynn and Whitcomb 1987) specimens. The inventories given in Appendix I are summations of cleared and uncleared specimens. We feel that the risk of misdeterminations of uncleared specimens is very low, with some important caveats. Females of the *prairiana* and *flexulosa* groups must be cleared for determination, and males of the *prairiana* group should be cleared. In many cases large series were available, in which case we cleared several specimens and tentatively identified others by inference. For these reasons the numbers given probably are an accurate reflection of the relative abundance of each species. We attempted to curate the collections examined and to supplement them, where possible, with additional material.

IPL ACCESSIONS.—The BARC collection is largely computerized (Lynn and Whitcomb 1987); collection records are given in terms of the accession number in this system. Collection methods have been described (Whitcomb et al. 1986, 1987).

ORIGINAL BEAMER FIELD NOTES.—Relevant excerpts from field notes written by Mrs. Lucy D. Beamer on:

*ritana*. "08-18-35. Santa Rita Mts., Ariz. (E. side) 11:30–5 PM. mild, fair to cloudy . . . Dr. Ball, RHB (R. H. Beamer) and Jack climbed the trail up the mountain. Just as they were abandoning the search RHB took a new species of *Gladionura* or *Athysanella* which Dr. Ball is naming. Worked for a good while, finally had 30 or 40 of them. Before this only 3 specimens had been taken." There are no explicit references to *Flexamia*, or to the exact collecting location. The *Athysanella* species mentioned was presumably *A. (Gladionura) furculata*.

*beameri*. "07-26-46. Otter Lake, New York (5 miles west). Collected just inside Adirondack Park on Highway 365 at one of the first little lakes. R. [R. H. Beamer] swept tiny sedges along the shore—took 80 or so of a tiny fulgorid he thought was *Bakerella* sp. Later not so sure." Again, there was no explicit mention of *Flexamia*.

Unidentifiable female. "08-07-37. Cowan, Manitoba (3 miles north). R. swept in the tall green grass growing up through the heavy mat of fallen grass which surrounds a lake for fifty or a hundred yards in all directions. Found interesting cicadellid—long wings—probably belonging to the genus *Polyamia*. Their wings were ruffed even when he took them." We have been unable to find other specimens from this collection in the KU collection.

# *AFRONISIA*, A NEW AFRICAN GENUS OF MEENOPLIDAE (HOMOPTERA: FULGOROIDEA)

Michael R. Wilson[1]

ABSTRACT.—The new genus *Afronisia* is founded with *Eponisia albovittata* Fennah as the type-species. *Eponisia brunnescens* Synave, *E. flavescens* Synave, *E. pallida* Linnavuori, and *Nisia muiri* Metcalf are transferred to this genus, and *E. albinervosa* Muir is placed in synonymy with *Kermesia albinervosa* Muir. Two new species are described: *Afronisia bredoi*, from Zaire, and *A. gembuensis*, from Nigeria. Keys are provided for separation of the African genera of Kermesiinae and for the seven species of *Afronisia* that are described and figured.

The Old World planthopper family Meenoplidae is one of the smaller fulgoroid families, consisting of slightly more than 100 described species. Until recently all species were placed in eight genera in two subfamilies, the Meenoplinae and the Kermesiinae (=Nisiinae). However, Emeljanov (1984) and Tsaur et al. (1986) described new genera for existing species in the Oriental region and named several new species. Over 50 species are known from Africa through the work of Muir (1927, 1934) and other early workers and, more recently, by Fennah (1955, 1957, 1958), Linnavuori (1973), and Synave (1957a, 1957b, 1971). It is now apparent that only a small proportion of the species has been described so far, as has been found for other African fulgoroid groups (e.g., Derbidae, Wilson 1987).

Meenoplids are small fulgoroids with tentiform forewings and one or both claval veins with sensory pits ("granulations" in older literature) on either side of the vein. Females possess wax-producing plates on abdominal segments 6–8. The family belongs to a group that includes Achilixiidae, Kinnaridae, and Achilidae. Meenoplidae are divided into two subfamilies, the Meenoplinae and the Kermesiinae. In the Meenoplinae the first claval vein has a single row of sensory pits, and the second claval vein is more or less covered with them. In the Kermesiinae the claval veins are fused near the apex of the clavus (e.g., Fig. 4). The first claval vein has a row of sensory pits on either side of the vein. Three African genera are placed in this subfamily: *Kermesia*, *Nisia*, and *Afronisia*.

Kermesiinae was first used by Kirkaldy (1906:427) as a subfamily of Derbidae to include *Nisia*, *Phaconeura*, *Suva*, and several derbid genera. Although the subfamily was named Kermesiinae, the genus *Kermesia* was not treated at that time but was included by implication in comments on *Nisia* by Kirkaldy (1906:427), who stated that "[*Nisia*] seems hardly differentiated from *Kermesia*." However, in the following year Kirkaldy (1907:163) stated that two subfamilies of the Derbidae may be recognized, including the Nisiinae represented by *Nisia*. The name Nisiinae was accepted by most subsequent workers, including Metcalf (1945). Recently, Emeljanov (1984) and Tsaur et al. (1987) used Kermesiinae as the subfamily name in preference to Nisiinae; this name has been followed here.

The African meenoplid species have been placed in the genera *Nisia*, *Kermesia*, *Eponisia* (Kermesiinae), *Anigrus*, and *Meenoplus* (Meenoplinae). Because these genera are all poorly defined, it is necessary for several new genera to be erected to accommodate some existing species and some undescribed ones. The five African species currently placed in *Eponisia* have little in common with the remaining Asiatic species, which include the type-species, *E. guttula* Matsumura, described from Taiwan (Tsaur et al. 1986). This has also been noted by Emeljanov (1984). The present paper transfers four of them to *Afronisia* and the fifth to synonymy in *Kermesia*.

## Abbreviations of Depositories

BMNH British Museum (Natural History), London, UK
IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium

[1]CAB International Institute of Entomology, c/o Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, UK.

MNHN Museum National d'Histoire Naturelle, Paris, France
MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NCI National Insect Collection, Pretoria, South Africa
RL R. Linnavuori Collection, Raisio, Finland

Key to African Genera of Kermesiinae

1. Clypeus rounded, without lateral carinae. Forewing with only one branch to M apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Nisia*
— Clypeus with lateral carinae. Forewing with two branches of M at apex (Fig. 4) . . . . . . . . . . . . . . . 2
2(1). Eyes large, twice as long as wide. Forewing with clavus more than half total length. Hind tarsal segments with segment 1 approximately equaling in length segments 2 + 3 . . . *Afronisia* gen. n.
— Eyes smaller, only slightly longer than wide. Forewing with clavus one-third total length. Hind tarsal segment 1 longer than 2 + 3 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Kermesia*

## *Afronisia*, gen. n.

TYPE-SPECIES.—*Eponisia albovittata* Fennah.

DESCRIPTION.—Small, slender meenoplids, length overall 3.5–5.9 mm. Head with vertex longer than wide, merging smoothly into frons with profile strongly rounded, posterolateral areolets widely spaced. Frons over twice as long as broad; lateral carinae parallel for most of their length, diverging slightly on clypeus, interrupted at frontoclypeal suture. Clypeus with lateral carinae extending from lateral carinae of frons; median carinae weakly developed but present toward rostrum. Rostrum long, extending beyond hind trochanters. Pronotum with well-defined anterior carina parallel to the anterior margin, carina also present on shoulder of pronotum. Mesonotum with median carina present but not sharply defined, lateral carinae obscure.

Forewing: Relatively long and narrow, 2.5–3.0 times longer than maximum width, clavus longer than half total length. Sc + R united for almost half wing length, R bifurcate at apex, M bifurcate at apex. Claval veins appear to join inner margin before apex of clavus but actually enter the apex.

Hindwing: r-m crossvein at approximately half length of wing, R and M bifurcate at apex.

Hindlegs: Hind tibiae with lateral spines. Posttibia with 8 spines grouped as 3 + 5. Apex of segment 1 with approximately 8 spines, median ones less sclerotized than other ones. Apex of segment 2 with similar arrangement of spines. Tarsal segment 1 approximately equal in length to segments 2 + 3.

MALE GENITALIA.—Pygofer dorsoventrally elongated, in lateral view with dorsolateral angle slightly or strongly produced, either rounded or pointed. Anal segment with lateral margins diverging apically, posterolateral angles produced or rounded. Aedeagus (phallus) tubular, enlarged at apex, more or less trumpet-shaped. Periandrium (phallobase) with several pairs of appendages arising from base, inner pairs more slender than outer pairs. Parameres long and narrow, apical portion upcurved.

FEMALE GENITALIA.—Of the "reduced" meenoplid form.

DISTRIBUTION.—Africa south of Sahara.

DIAGNOSIS.—The genus may be distinguished from *Nisia* and *Kermesia* by the following characters. In *Nisia* the lateral carinae of the clypeus are absent; they are present in *Afronisia* and *Kermesia*. In *Kermesia* the carinae extend smoothly from the frons; in *Afronisia* they are disjunct. The eyes of *Afronisia* species are large, twice as long as wide, while in *Kermesia* and *Nisia* they are more globular. The forewing venation in *Afronisia* differs, with the clavus more than half the length of the forewing and M bifurcate at its apex. In *Kermesia* M is also bifurcate, but the clavus is short, only one-third the length of the forewing. In *Nisia* M is single at its apex, with the clavus more or less half the length of the forewing. The hind tarsal segment 1 is longer than 2 + 3 in both *Nisia* and *Kermesia* and is more or less equal to the length of 2 + 3 in *Afronisia*. All of these features are at present only diagnostic. However, the appendages of the aedeagus are characteristic and are not present in other meenoplid genera but are here regarded as apomorphic for the genus. Oriental species of *Eponisia* resemble *Kermesia* in some respects and differ markedly from *Afronisia* in the form of the male genitalia (Tsaur et al. 1987).

The biology and host plants are little known. Linnavuori (1973) records *A. albovittata* (Fennah) and *A. brunnescens* (Synave) as being collected "in a swamp."

Key to Species (Males) of *Afronisia*

1. Forewing almost entirely dark brown, contrasting strongly with yellow, dorsal stripe from vertex to pronotum and mesonotum. Aedeagus

with 3 pairs of processes (Fig. 7) ............ ........................ *albovittata* (Fennah)

— Forewing variable in color but never entirely dark brown. Aedeagus with between 2 and 4 pairs of processes ........................ 2

2(1). Aedeagus with 2 pairs of large, sclerotized processes ................................ 3

— Aedeagus with 3 or 4 pairs of processes (Figs. 22, 35, 45) ................................ 4

3(2). Forewings overall pale whitish gray. Aedeagus with outer processes very large, curved, extending beyond phallus (Fig. 56), short, central process present .................... *bredoi*, n. sp.

— Forewing with white veins, membranes pale brown (Fig. 15). Aedeagus with outer processes shorter than phallus, short, central process absent .......................... *muiri* (Metcalf)

4(2). Aedeagus with 4 pairs of processes (Fig. 22) ... ......................... *flavescens* (Synave)

— Aedeagus with 3 pairs of processes ........... 5

5(3). Aedeagus with outer pair of processes longer than inner pairs, curved inward and dorsad (Figs. 33–35). Pygofer with laterodorsal angles pointed (Fig. 31) ......... *brunnescens* (Synave)

— Aedeagus with outer pair of processes shorter than inner pairs, pygofer with laterodorsal angles rounded ............................ 6

6(5). Outer pair of aedeagal processes short and bifurcate (Fig. 50) ............... *gembuensis*, n. sp.

— Outer pair longer, about two-thirds length of inner pairs (Fig. 45) ......... *pallida* (Linnavuori)

## *Afronisia albovittata* (Fennah), comb. n.
Figs. 1–12

*Eponisia albovittata* Fennah 1955. Ann. Mus. Congo Tervuren in ser. 8. Zool. 40: 434.

LENGTH.—Male 4.2–4.4 mm, female 4.5–4.8 mm.

DESCRIPTION.—Coloration: Overall dark brown species. Vertex and face with lateral edges of carinae dark brown, face between carinae brown or light yellow in some specimens, becoming yellow at junction of face and vertex. Antennae dark brown, eyes dark. Vertex pale yellow. Pronotum and mesonotum with central, yellow stripe (Fig. 1) with orange pigmentation following median carina. Forewing dark brown, inner margin of clavus and subapical line of transverse veins between R and Cu and between apex of clavus and $Cu_1$ white (Fig. 4). Legs brown. Abdomen and genital capsule dark brown.

MALE GENITALIA (Figs. 7–12).—Pygofer longer than broad, laterodorsal angles acute (Fig. 10). Anal segment with apical (posterior) margin concave between rounded posterolateral margins (Fig. 11), slightly deflexed in lateral view (Fig. 10). Aedeagus with periandrium bearing three pairs of sclerotized processes from ventral portion (Fig. 7), the outer pair broader and slightly shorter than the inner pair and central pair very short. Long, trumpet-shaped central portion (phallus) extending beyond processes. Parameres long, with upcurved, subspinose, apical process (Fig. 9), slightly widened before apical portion in dorsal view (Fig. 12).

DISTRIBUTION.—East Africa: Rwanda (type locality), Sudan (Equatoria Prov.) (Linnavuori 1973), Uganda, Kenya, Zaire.

MATERIAL EXAMINED.—Males and females from Kenya, Uganda, Sudan (Equatoria Prov.) (BMMH).

REMARKS.—Fennah's original description (1955) states that the phallobase (periandrium) possesses two pairs of sinuate spines, not three as actually present. However, Fennah's drawing was made from a lateral view, and the short, central (ventral) pair may not have been visible. The male genitalia were figured correctly by Synave (1957b) from material from the type locality, and for this reason the type-specimen was not reexamined.

DIAGNOSIS.—The dark coloration of the species and the pale yellow, dorsal stripe distinguish it from all others in the genus.

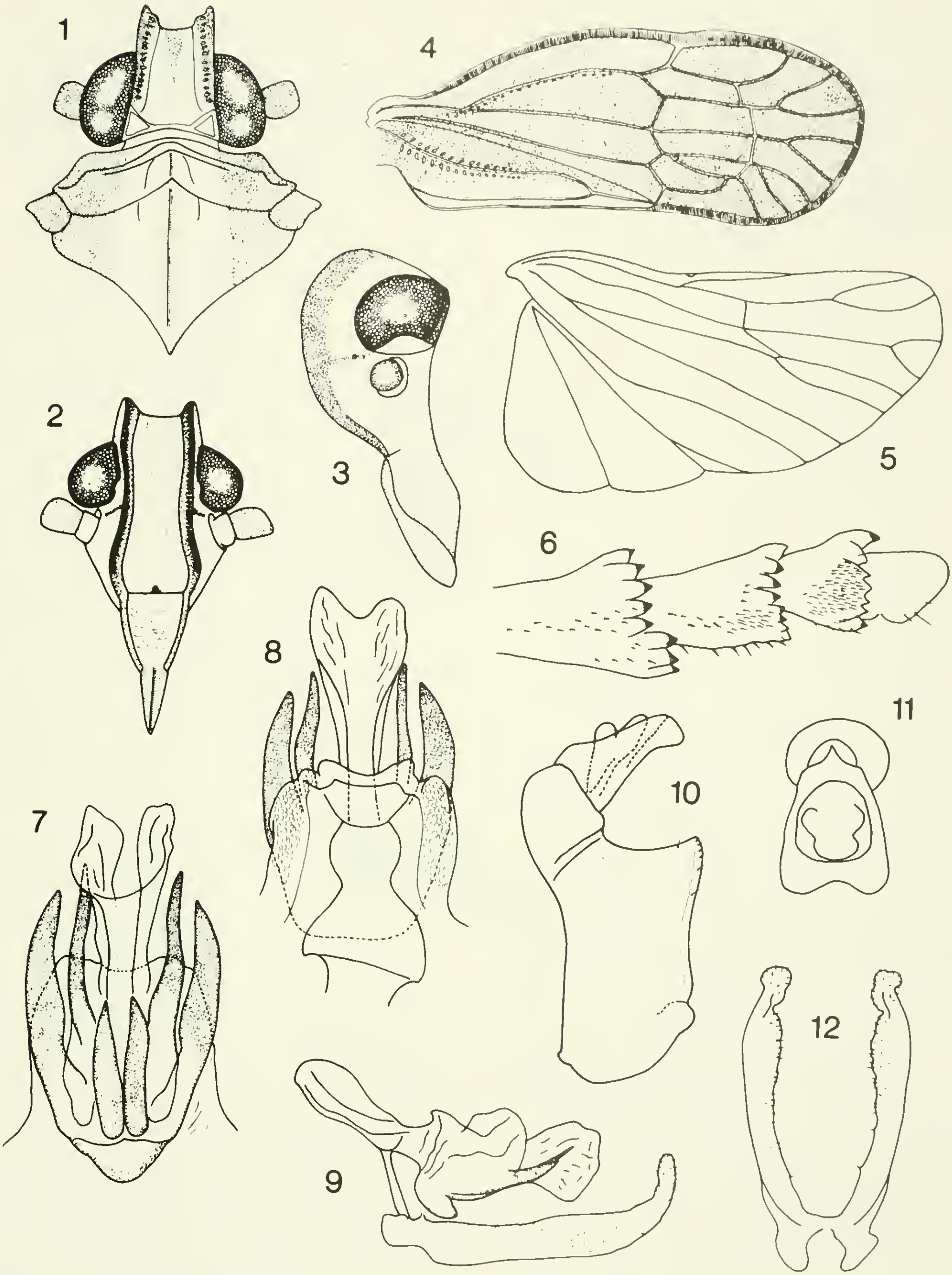
## *Afronisia muiri* (Metcalf), comb. n.
Figs. 13–21

*Nisia albovenosa* Muir 1927. Ann. Mag. Nat. Hist. (9)19: 200. [Preoccupied by *Nisia albovenosa* Distant, 1906] *Nisia muiri* Metcalf 1945: 228 replacement name for *Nisia albovenosa* Muir.

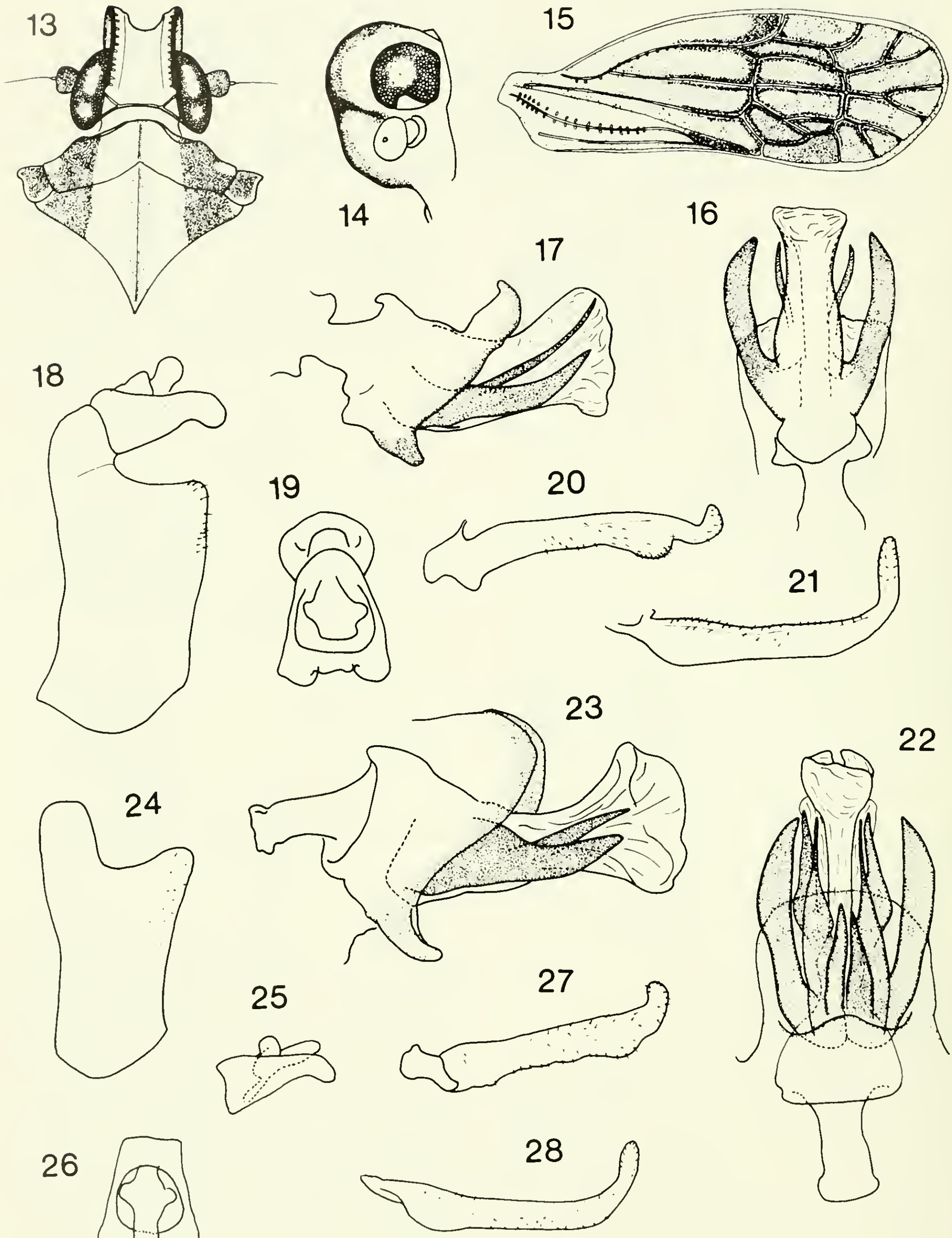
LENGTH.—Male 3.5–3.8 mm, female 4.5–4.6 mm.

DESCRIPTION.—Coloration: Lateral carinae of head and vertex dark brown. Face and clypeus brown, lateral carinae of clypeus pale. Vertex pale yellow-white. Pronotum and mesonotum with lateral margins brown with central, pale stripe (Fig. 13), median carina narrowly orange. Forewing with veins white, membranes light brown, darker adjacent to veins (Fig. 15), granulations dark brown on white background. Abdomen dark brown, intersegmental membranes white. Legs light brown.

MALE GENITALIA (Figs. 16–21).—Pygofer longer than broad, laterodorsal angles almost rectangular (Fig. 18). Anal segment posteriorly deflexed in lateral view (Fig. 18), slightly




Figs. 1–12. *Afronisia albovittata* (Fennah): 1, head and thorax, dorsal view; 2, head, face; 3, head, lateral view; 4, forewing; 5, hindwing; 6, hindleg; 7, aedeagus, ventral view; 8, aedeagus, dorsal view; 9, aedeagus and parameres, lateral view; 10, pygofer and anal segment, lateral view; 11, anal segment, dorsal view; 12, parameres, ventral view.




Figs. 13–28. Figs. 13–21, *Afronisia muiri* (Metcalf): 13, head and thorax, dorsal view; 14, head, lateral view; 15, forewing; 16, aedeagus, ventral view; 17, aedeagus, lateral view; 18, pygofer and anal segment, lateral view; 19, anal segment, dorsal view; 20, paramere, ventral view; 21, paramere, lateral view. Figs. 22–28, *Afronisia flavescens* (Synave): 22, aedeagus, ventral view; 23, aedeagus, lateral view; 24, pygofer, lateral view; 25, anal segment, lateral view; 26, anal segment, dorsal view; 27, paramere, ventral view; 28, paramere, lateral view.

produced posterior processes (Fig. 19). Aedeagus with periandrium bearing two pairs of sclerotized processes (Fig. 16), outer pair large, curved, inner pair longer, thin (Fig. 17). Parameres with upturned apical portion (Fig. 21), subapical lobe in dorsal view (Fig. 20).

DISTRIBUTION.—South Africa.

MATERIAL EXAMINED.—Holotype ♀, SOUTH AFRICA, Port St. John, Pondoland, R. E. Turner, iv.1923 (BMNH); 1 ♀, same data as holotype; 1 ♂ 6 ♀, Rustenburg, Transvaal, 10–13.xii.1961 (Capener); 1 ♀, Trazaneen, Transvaal, 10.xii.1918; 1 ♀, Umtentweni, Natal, 9–14.iii.1961 (Capener) (NCI, 2 ♀ BMNH); 1 ♂, Ladysmith, 29.i.1981 (Theron); 1 ♀, Dundee, 21.i.1981 (Theron); 1 ♀, Durban, 7.i.1971 (Kluge) (BMNH).

REMARKS.—The species was originally described from one female. A second female from the same locality (Port St. John, Pondoland) is also present in the BMNH collection. Only two males were present among the specimens from South Africa. No further species have been found in South Africa. Comparison of wing pigmentation supports the association of the males with the type female. Synave (1957b) repeated Muir's original description but did not examine the type-specimen.

DIAGNOSIS.—This is the only species known at present from South Africa. The forewing coloration is distinctive, and the male aedeagus is characteristic with the two pairs of processes.

### *Afronisia flavescens* (Synave), comb. n.
Figs. 22–28

*Eponisia flavescens* Synave 1971. Bull. Inst. r. Sci. nat. Belg. 47(39): 10.

LENGTH.—Male 4.2 mm, female 4.8 mm.

DESCRIPTION.—Coloration: Male head and body orange, pale yellow stripe on pronotum and mesonotum with orange median pigmentation following median carina. Lateral carinae of head edged dark brown. Legs orange.

Forewing with veins white, apices pale brown. Membranes suffused, very pale brown. Granulations with black points on white background.

Female much paler than male. Overall stramineous.

MALE GENITALIA (Figs. 22–28).—Pygofer with laterodorsal angles acute (Fig. 24). Anal segment deflexed posteriorly in lateral view (Fig. 25), posterior margin scarcely produced (Fig. 26). Aedeagus with periandrium with four pairs of sclerotized processes (Fig. 22), outer pair thickest, two inner pairs thinner but more or less equal in length, central pair about half the length. Central portion (phallus) longer than processes (Fig. 22). Parameres as in other species with upturned apical portion (Figs. 27, 28).

DISTRIBUTION.—Nigeria.

MATERIAL EXAMINED.—Holotype ♂, NIGERIA, Badeggi, N.W. State (IRSNB). Paratype ♀ (not male as stated in original description), NIGERIA, Yankar, N.E. State (IRSNB).

DIAGNOSIS.—A pale species, similar in coloration to *A. bredoi* n. sp. The only species to have four distinct pairs of aedeagal processes.

REMARKS.—Known only from the type material.

### *Afronisia brunnescens* (Synave), comb. n.
Figs. 29–37

*Eponisia brunnescens* Synave 1957a. Expl. Parc National de l'Upemba. Fasc. 43(2): 7.

LENGTH.—Overall male 4.2–4.4 mm, female 4.6–4.9 mm.

DESCRIPTION.—Coloration: Male body and legs pale orange. Vertex and mesonotum with distinct, pale yellow stripe, darker orange laterally. Edges of lateral carinae of head dark brown extending to lateral ocellus, inner margin (sensory pits) whitish. Antennae pale yellow brown.

Forewing: Membranes pale, stramineous, light brown, darker adjacent to veins. Veins white, with apices darker. Claval vein with sensory pits dark brown. Forewing narrow, parallel-sided, rounded at apex.

Hindwing: Whitish, veins pale brown.

Female paler generally than male.

MALE GENITALIA (Figs. 31–37).—Pygofer with laterodorsal angles extended, acute in profile (Fig. 31). Anal segment with posterolateral apical lobes reflexed (Figs. 31, 32). Aedeagus with periandrium bearing three pairs of sclerotized processes, the outer pair longer and thicker than two inner pairs, curved inward and dorsad apically (Figs. 33–35), inner pair diverging apically (Figs. 33, 35), central pair short, about half the length of outer pairs. Phallus longer than processes, trumpet-shaped. Parameres slender, apical quarter directed dorsad (Fig. 36). Some

variation appears in length of processes (Fig. 33 illustrates the paratype, Fig. 35 is a specimen from Cameroon).

DISTRIBUTION.—Central and west Africa: Cameroon, Sudan (Equatoria Prov.) (Linnavuori 1973), Zaire (Katanga Prov., type locality, Orientale Prov.), Central African Republic (Bossangoa).

MATERIAL EXAMINED.—Holotype ♂, ZAIRE, Kaziba (MRAC). Paratype ♂, ZAIRE, Kabwe (MRAC). ZAIRE, numerous specimens from Parc National de la Garamba (northeast Zaire) (IRSNB, MRAC); 1 ♂, CAMEROON (Banyo) (BMNH); 1 ♂, CENTRAL AFRICAN REPUBLIC (Bossangoa) (RL).

DIAGNOSIS.—The male genitalia are very characteristic with the curved outer pair of processes. The species was found mixed in series with *A. pallida* and may be separated by the narrow, parallel-sided forewings as well as by the male genitalia.

### *Afronisia pallida* (Linnavuori), comb. n.
Figs. 38–45

*Eponisia pallida* Linnavuori 1973. Notul. ent. 53: 111.

LENGTH.—Overall male 4.5–5.0 mm, female 5.2–5.8 mm.

DESCRIPTION.—Coloration: Male/female, lateral carinae of head with edges dark brown, body and head pale yellow, mesonotum orange laterally, pale, median stripe interrupted by orange, median carina. Legs pale yellow. Abdomen and genital capsule stramineous. Forewing with pale yellow membrane, white veins, apices of veins marked with brown (Fig. 38), apical cells darkened adjacent to veins, black tips to white sensory pits on claval veins. Forewing becoming broader toward apex.

MALE GENITALIA (Figs. 40–45).—Pygofer with laterodorsal angles broadly rounded in profile (Fig. 41), anal segment with posterolateral lobes (Fig. 40) reflexed (Fig. 41). Aedeagus (Figs. 45, 46) with periandrium bearing three pairs of sclerotized processes and one central (ventral) process, outer pair shorter than inner pairs (Fig. 45), the more dorsal of the inner pairs converging apically (Fig. 45), the inner pair parallel for half their length before diverging (Fig. 45), single, central spine short. Two small spines on dorsal surface of phallus. Parameres with distinct ventral lobe one-third distance from apex with apical third curved upward and twisted (Figs. 42, 43).

DISTRIBUTION.—Central Africa: Sudan (Equatoria Prov., type locality) (Linnavuori 1973), Central African Republic, Zaire.

MATERIAL EXAMINED.—Holotype ♂, SUDAN, Equatoria, Yambio (RL). Paratype ♀, SUDAN, Equatoria, Yambio (BMNH). CENTRAL AFRICAN REPUBLIC (Bossangoa) (IRSNB). ZAIRE, numerous specimens from Parc National de la Garamba (northeast Zaire) (IRSNB, MRAC).

REMARKS.—Found in same localities as *A. brunnescens* since it is mixed in collections from Zaire.

DIAGNOSIS.—A pale species, externally similar to *A. brunnescens* but slightly larger and with forewings broadened rather than parallel-sided. Male genitalia very distinct with three pairs of long processes.

### *Afronisia gembuensis*, n. sp.
Figs. 46–51

LENGTH.—Male 4.7 mm, female 5.2 mm.

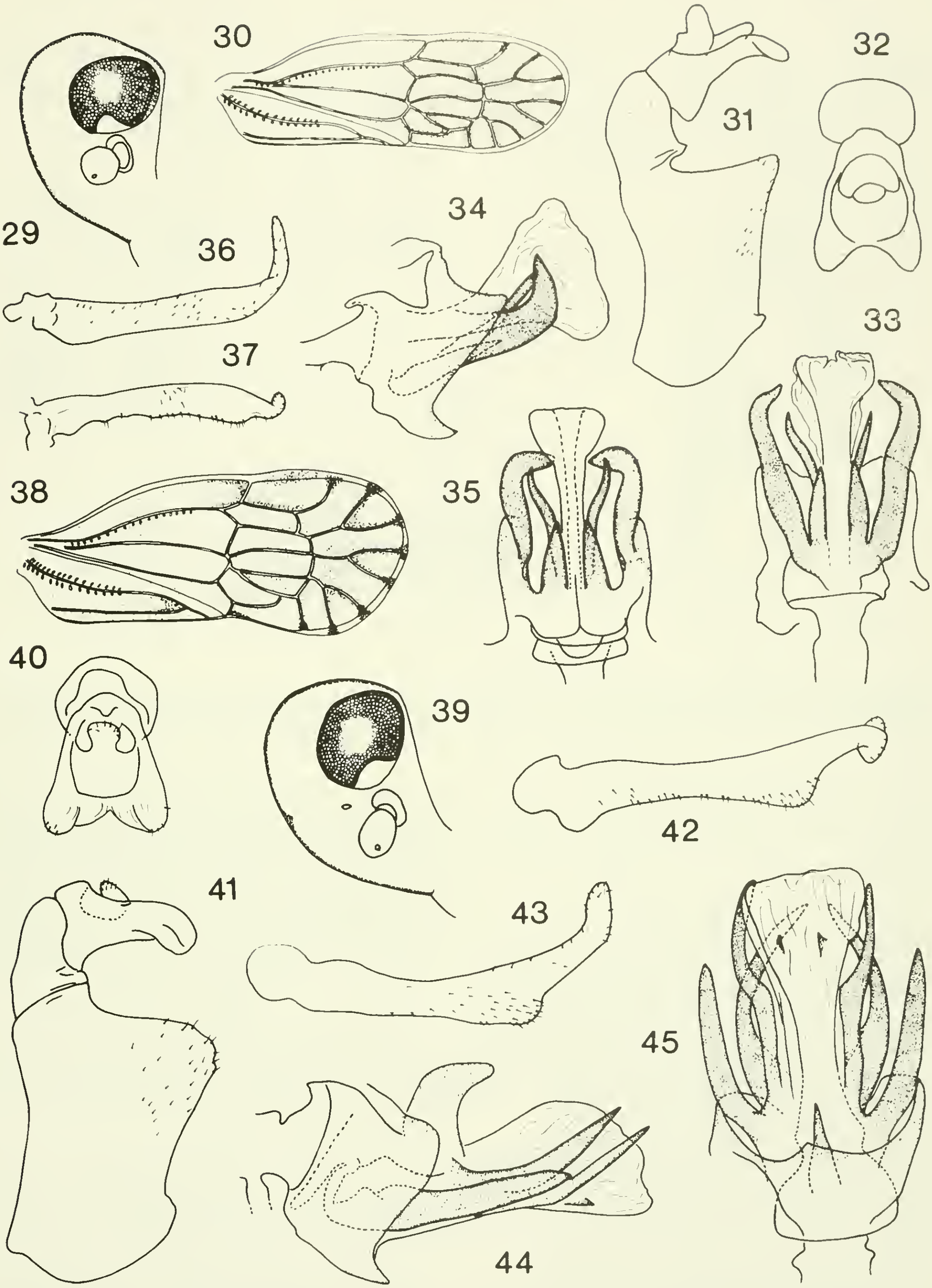
DESCRIPTION.—Body color pale orange, resembling *A. muiri*, especially in darker pigmentation of forewings.

MALE GENITALIA (Figs. 46–51).—Pygofer with laterodorsal angles rounded (Fig. 46). Anal segment with lateral margins diverging apically, posterolateral angles acute (Fig. 47), with apical margin concave. Aedeagus with periandrium with three pairs of sclerotized processes and one short, central process, outer pair short and bifurcate (Fig. 50), inner pairs long, with outer of these diverging, inner one almost parallel (Fig. 50), central process short. Parameres with pronounced ventral lobe two-thirds as long as its length, apical third thinner and directed dorsad, slightly twisted (Figs. 48, 49).

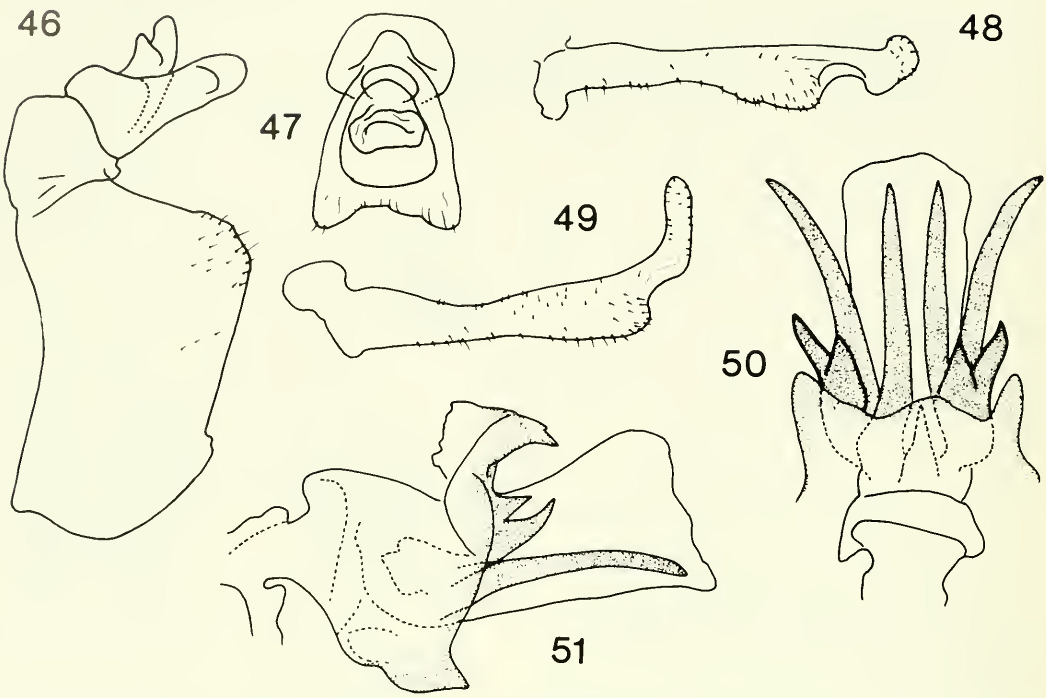
DISTRIBUTION.—Nigeria.

TYPE MATERIAL.—Holotype ♂, NIGERIA, N.E. State, Gembu-Yelwa, 22.viii.1973, Linnavuori (RL). Paratypes, 3 ♂ 6 ♀, NIGERIA, N.E. State, Gembu, 21–22.viii.1973, Linnavuori (RL, 1 ♂ 1 ♀ deposited in each BMNH, MRAC).

DIAGNOSIS.—Somewhat similar to *A. pallida* in aspects of the male genitalia and particularly in the shape of the laterodorsal angles of the pygofer and the shape of parameres. The aedeagal (periandrium) processes are, however, diagnostic, particularly the bifurcated outer pair.




Figs. 29–45. Figs. 29–37, *Afronisia brunnescens* (Synave): 29, head, lateral view; 30, forewing; 31, male pygofer and anal segment, lateral view; 32, anal segment, dorsal view; 33, aedeagus, ventral view, paratype; 34, aedeagus, lateral view; 35, aedeagus, ventral view; 36, paramere, lateral view; 37, paramere, ventral view. Figs. 38–45, *Afronisia pallida* (Linnavuori): 38, forewing; 39, head, lateral view; 40, male anal segment, dorsal view; 41, pygofer and anal segment, lateral view; 42, paramere, ventral view; 43, paramere, lateral view; 44, aedeagus, lateral view; 45, aedeagus, ventral view.




Figs. 46–51. *Afronisia gembuensis*, n. sp.: 46, male pygofer and anal segment, lateral view; 47, anal segment, dorsal view; 48, paramere, ventral view; 49, paramere, lateral view; 50, aedeagus, ventral view; 51, aedeagus, lateral view.

## *Afronisia bredoi*, n. sp.

Figs. 52–57

LENGTH.—Male 5.2 mm, female 5.7–5.9 mm.

DESCRIPTION.—Coloration male/female: body and legs light orange dusted with wax. Head with lateral carinae of vertex and face edged with dark brown, face suffused with light brown. Mesonotum/pronotum light orange laterally, central, pale yellow stripe with median carina light orange. Antennal scape very pale brown, pedicel darker.

Forewing: Overall pale grey-white, membranes darker, particularly adjacent to veins. Apices of veins at margin darker, especially in female. Forewing distinctly wider toward apex.

MALE GENITALIA (Figs. 52–57).—Pygofer with laterodorsal angles rounded (Fig. 52). Anal segment with lateral margins diverging apically, posterolateral angles produced (Fig. 53). Aedeagus with periandrium bearing two pairs of sclerotized processes, and a single, central one, outer processes very large, curved inward beyond the phallus, with short processes arising laterally at base. These are asymmetric in specimen examined (Fig. 56). Inner processes shorter than phallus, more or less parallel, central spine short. Parameres with apical third curved smoothly upward in lateral view (Fig. 57), twisted apically (Fig. 54).

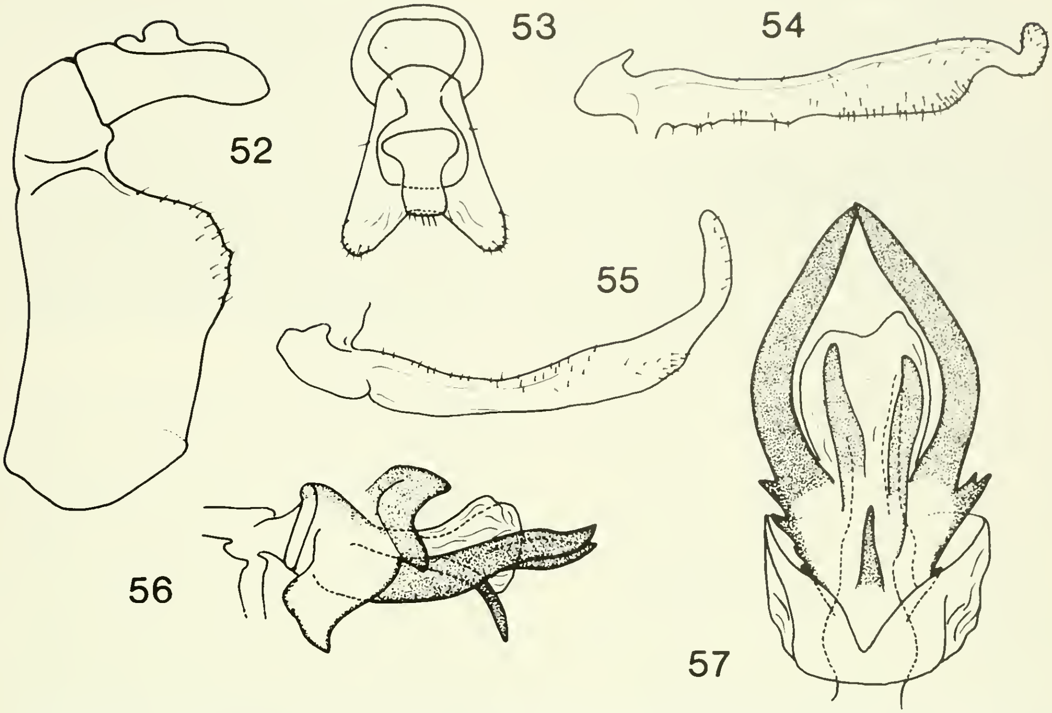
DISTRIBUTION.—Zaire (Elisabethville).

TYPE MATERIAL.—Holotype ♂, ZAIRE, labeled Congo Belge, Elisabethville, iv.1939, H. J. Bredo (MRAC). Paratypes: 2 ♀, same data as holotype (MRAC).

DIAGNOSIS.—A pale-colored species resembling *A. pallida*. The long, curved, outer appendages of the male aedeagus are diagnostic and resemble no other species.

### Remarks on *Eponisia albinervosa* Muir 1934

This species is considered the junior synonym of *Kermesia albinervosa* Muir 1927 (type locality, Sierra Leone). The male holotype and female allotype were very badly damaged in transit from Honolulu to London




Figs. 52–57. *Afronisia bredoi*, n. sp.: 52, male pygofer and segment, lateral view; 53, anal segment, dorsal view; 54, paramere, ventral view; 55, paramere, lateral view; 56, aedeagus, lateral view; 57, aedeagus, ventral view.

in 1927 (together with other African meenoplid types described in the same paper). Fortunately, the male genitalia of the holotype were intact and other specimens have been associated. It is with these specimens that the female holotype of *Eponisia albinervosa* from Uganda has been compared.

The synonymy is as follows:

*Kermesia albinervosa* Muir 1927. Ann. Mag. Nat. Hist. (9)19: 203.

*Eponisia albinervosa* Muir 1934. Ann. Mag. Nat. Hist. (10)14: 564. *syn. n.*

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# DELPHACIDAE OF ALASKA (HOMOPTERA: FULGOROIDEA)

Stephen W. Wilson[1]

ABSTRACT.—Fifteen species, in 10 genera, of Delphacidae are recorded from Alaska. One, *Kusnezoviella macleani*, is described as new to science. *Acanthodelphax analis* (Crawford), *Chilodelphax magnifrons* (Crawford), *Javesella arcanastyla* (Beamer), and *J. atrata* (Osborn) are new combinations. *Delphacodes saileri* Beamer is a synonym of *Javesella simillima* (Linnavuori).

Of the 15 species, 1 is recorded only from Alaska, 3 are Holarctic, 4 are Nearctic, and 7 are Palearctic and restricted to tundra habitats, with 5 of these apparently found only north of the Brooks Range.

Little information is available on species diversity and distribution of much of the Alaskan insect fauna (MacLean and Hodkinson 1980). For example, only seven species of Delphacidae have been described from Alaska. *Delphacodes stejnegeri* (Ashmead) was described by Ashmead (1904) and redescribed and illustrated by Dozier (1926). Vilbaste (1980) synonymized this species with *Javesella pellucida* (Fabricius). *Delphacodes atrata* Osborn was recorded from Alaska by Beamer (1951). *Delphacodes saileri* Beamer (1952b) was described from Alaska but, as indicated below, is a synonym of *Javesella simillima* (Linnavuori). DuBose (1960) recorded the Holarctic *D. pellucida* from Alaska. *Delphacodes uniformis* (Walker) was listed from Alaska by Metcalf (1943); however, Muir (1919) stated that this insect is not a delphacid. *Megamelus flavus* Crawford was recorded from Alaska by Beamer (1955).

The present paper provides a key and information on distribution for the 15 delphacid species found in the Canadian National Collection, Ottawa, and material collected by MacLean in the northern part of the state. The name used by the first describer and the first placement in the current genus are given for each species. Because the species have been described in detail elsewhere, only the new species of *Kusnezoviella* is described. Accurate identification of delphacids relies on use of characters of the male genitalia; for this reason, all species treated here are illustrated.

Key to the Alaskan Delphacidae

1. Frons with 2 longitudinal, median carinae (Fig. 1) . . . . . . . . 2

— Frons with 1 longitudinal, median carina . . . . 3

2(1). Large pits present on frons, pronota, mesonota, and abdomen (Figs. 1, 2); aedeagus strongly decurved with poorly developed teeth (Figs. 2, 4) . . . . . . . . *Achorotile subarctica* Scudder

— Pits absent; aedeagus straight with well-developed teeth (Figs. 6, 7) . . . . *Criomorphus wilhelmi* Anufriev & Averkin

3(1). Pronotal lateral carinae straight, extending to, or almost to, posterior margin of pronotum (Fig. 12); metatibial spur with or without black-tipped teeth . . . . . . . . 4

— Pronotal lateral carinae curving laterad, not extending to posterior margin of pronotum; metatibial spur with black-tipped teeth, these sometimes weak . . . . . . . . 5

4(3). Metatibial spur with well-developed, black-tipped teeth; pygofer with lateral, inflated lobes (Figs. 9, 11) . *Megamelus flavus* Crawford

— Metatibial spur lacking teeth; pygofer not inflated laterally (Fig. 13) . . . . *Nothodelphax eburneocarinatus* (Anufriev)

5(3). Broad, pale stripe usually bordering longitudinal, median carinae on vertex, pronotum, and/or mesonotum; pygofer with broad lobe laterally on caudal margin (Figs. 16, 21) . . . . . 6

— Broad, pale stripe not present; pygofer without broad lobe . . . . . . . . 7

6(5). Styles each with irregular teeth on broad apex (Fig. 20) . . . . . . . . *Unkanodes excisa* (Melichar)

— Styles each with acute apex (Fig. 23) . . . . . . . . *Chilodelphax magnifrons* (Crawford)

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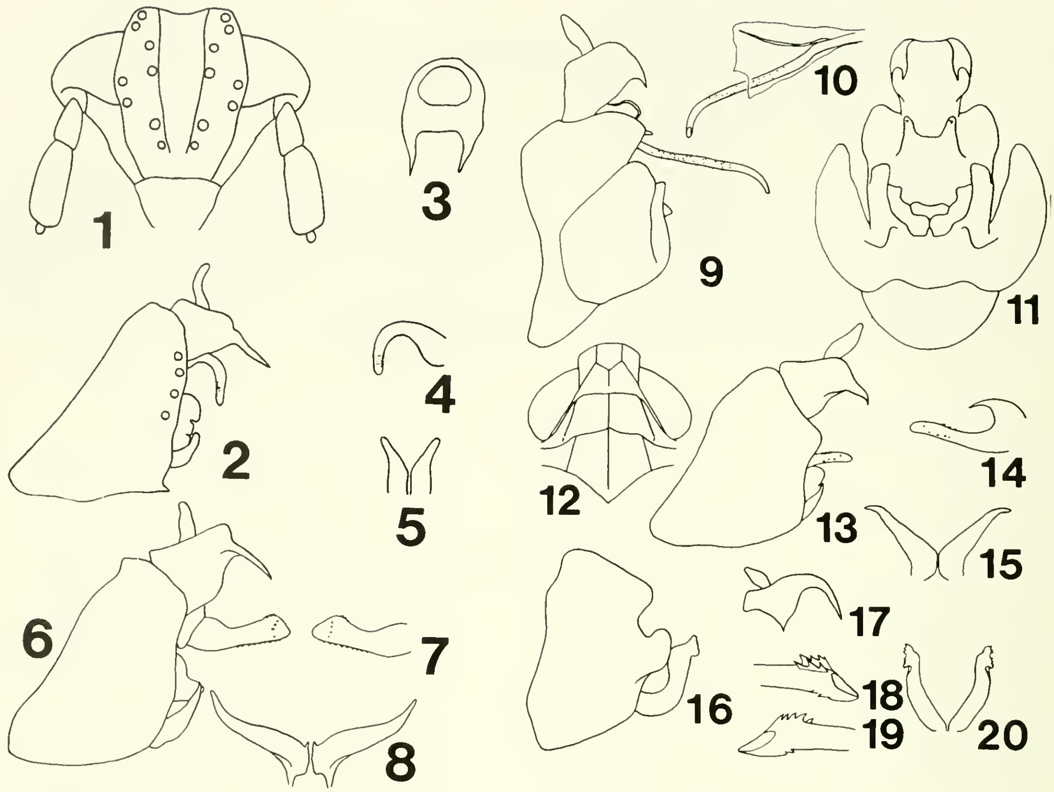



Figs. 1–20. Figs. 1–5, *Achorotile subarctica* Scudder: 1, head, frontal view; 2, male genitalia, lateral view; 3, anal tube, dorsal view; 4, aedeagus, lateral view; 5, styles, caudal view. Figs. 6–8, *Criomorphus wilhelmi* Anufriev & Averkin: 6, male genitalia, lateral view, 7, aedeagus, lateral view; 8, styles, caudal view. Figs. 9–11, *Megamelus flavus* Crawford: 9, male genitalia, lateral view; 10, aedeagus, lateral view; 11, male genitalia, caudal view. Figs. 12–15, *Nothodelphax eburneocarinatus* (Anufriev): 12, head and thorax, dorsal view; 13, male genitalia, lateral view; 14, aedeagus, lateral view; 15, styles, caudal view. Figs. 16–20, *Unkanodes excisa* (Melichar): 16, pyfoger and style, lateral view; 17, anal tube, lateral view; 18, 19, aedeagus, lateral view; 20, styles, caudal view.

7(5). Anal tube with spines crossing (Fig. 27) . . . . . . . . . . . . . *Ribautodelphax albostriatus* (Fieber)

— Anal tube with spines parallel or diverging . . 8

8(7). Pygofer with caudally directed, median projection ventral to base of styles (Fig. 29) . . . . . . . . . . . . . . . . *Acanthodelphax analis* (Crawford)

— Pygofer without median projection . . . . . . . . 9

9(8). Apices of styles converging (Fig. 34) . . . . . . . . . . . . . . . . . . . . . . *Kusnezoviella macleani*, n. sp.

— Apices of styles diverging . . . . . . . . . . . . . . . . 10

10(9). Aedeagus strongly decurved (Fig. 36) . . . . . . . . . . . . . . . . . . . . . *Javesella pellucida* (Fabricius)

— Aedeagus recurved or straight (Figs. 40, 43, 47, 50, 53) . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

11(10). Aedeagus evenly forked (Fig. 40) . . . . . . . . . . . . . . . . . . . . . . . . *Javesella obscurella* (Boheman)

— Aedeagus not forked (Figs. 43, 47, 50, 53) . . 12

12(11). Aedeagus with projection in basal half on ventral aspect (Figs. 50, 53) or with broad, weakly toothed region in basal half on ventral aspect (Fig. 47) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13

— Aedeagus not as above (Fig. 43) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Javesella atrata* (Osborn)

13(12). Aedeagus with large, ventral, basal projection (Figs. 50, 53) . . . . . . . . . . . . . . . . . . . . . . . . . 14

— Aedeagus without large, basal projection (Fig. 47) . . . . . . *Javesella simillima* (Linnavuori)

14(13). Aedeagal, ventral, basal projection acute, aedeagal dorsal margin slightly curved (Fig. 50) . . . . . . . . . . . . . *Javesella discolor* (Boheman)

— Aedeagal, ventral, basal projection rounded, aedeagal dorsal margin constricted (Fig. 53) . . . . . . . . . . . . . . . *Javesella arcanastyla* (Beamer)

## *Achorotile subarctica* Scudder

Figs. 1–5

*Achrotile* [sic] *subarctica* Scudder, 1963:169

Distribution records for specimens used in this study are: ALASKA: Brooks Range, Spruce

Tree Mine, 68°03′N, 149°W, 800 m, 4 July 1982, Seppo Keponen, ex. *B. glandulosa* (= *Betula glandulosa* Michx.) (1 male); White Mts., Eagle Summit, 900 m, 65°30′N, 145°25′W, 13 July 1982, Seppo Keponen, ex. *B. glandulosa* (1 male); Mt. Fairplay, Taylor Highway, 3,600 ft, 10 July 1962, P. J. Skitsko (1 male, 4 females); Happy Val., 15 June 1982, S. F. MacLean, tussock tundra (1 male, 2 females, 2 nymphs). Other records are from Anufriev and Averkin (1982a, 1982b), Anufriev and Emeljanov (1981), and Scudder (1963).

DISTRIBUTION.—NEARCTIC: Canada: Alberta, British Columbia, Northwest Territories; USA: Alaska. PALEARCTIC: Mongolia, USSR.

### *Criomorphus wilhelmi* Anufriev & Averkin
Figs. 6–8

*Criomorphus borealis* (Sahlberg), Anufriev 1972:613, 1977:864 nec Sahlberg
*Criomorphus wilhelmi* Anufriev and Averkin, 1982a:131; new name for *C. borealis* Anufriev nec Sahlberg

Distribution record for the specimen used in this study is: ALASKA: Unalakleet, 21 June 1961, R. Madge (1 male). Other records are from Anufriev (1972, 1977) and Anufriev and Averkin (1982a).

DISTRIBUTION.—NEARCTIC: Alaska. PALEARCTIC: Mongolia, USSR.

### *Megamelus flavus* Crawford
Figs. 9–11

*Megamelus notulus flavus* Crawford, 1914:609
*Megamelus flavus* Crawford: Beamer 1955:31

Specimens from Alaska were not available for this study; illustrations were made from a specimen with the following collecting data: WYOMING: Bighorn Nat'l. Park, Meadowlark Lake, 23 August 1954, M. W. Sanderson (1 male). Beamer (1955) recorded this species from Alaska but gave no further data. Other records are from Anufriev and Averkin (1982a), Beamer (1955), and Scudder (1964).

DISTRIBUTION.—NEARCTIC: Canada: Alberta, British Columbia, Manitoba, Northwest Territories, Quebec, Saskatchewan; USA: Alaska, Colorado, Wyoming. PALEARCTIC: Mongolia.

### *Nothodelphax eburneocarinatus* (Anufriev)
Figs. 12–15

*Tyrphodelphax eburneocarinatus* Anufriev, 1979:295
*Nothodelphax eburneocarinatus* (Anufriev): Emeljanov 1982:90
*Nothodelphax eburneocarinatus* (Anufriev): Anufriev and Averkin 1982a:137

Distribution records for specimens used in this study are: ALASKA: Alder Woodland, Arctic Circle, 66°33′N, 150°45′W, 17 June 1982, S. F. MacLean (7 males, 18 females); Brooks Range, Happy Valley, 69°05′N, 149°W, 320 m, 6 July 1982, Seppo Keponen, ex. *B. glandulosa* (1 male); Mt. Fairplay, Taylor Hwy., 3,600 ft, 10 July 1962, R. J. Skitsko (12 males, 54 females); Old Man Camp, 17 June 1982, S. F. MacLean (5 males, 21 females). Anufriev (1979) records it from sedge tussock bogs.

DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: USSR.

### *Unkanodes excisa* (Melichar)
Figs. 16–20

*Liburnia excisa* Melichar, 1898:67
*Elymodelphax excisa* (Melichar): Wagner 1963:167
*Unkanodes* (= *Elymodelphax*), Dlabola 1965:86

Distribution records for specimens used in this study are: ALASKA: Cape Thompson, 6 August 1979, S. F. MacLean (7 males, 8 females, 2 nymphs). Other records are from Nast (1972). This species was reported from *Elymus arenarius* L. in coastal habitats by Ossiannilsson (1978).

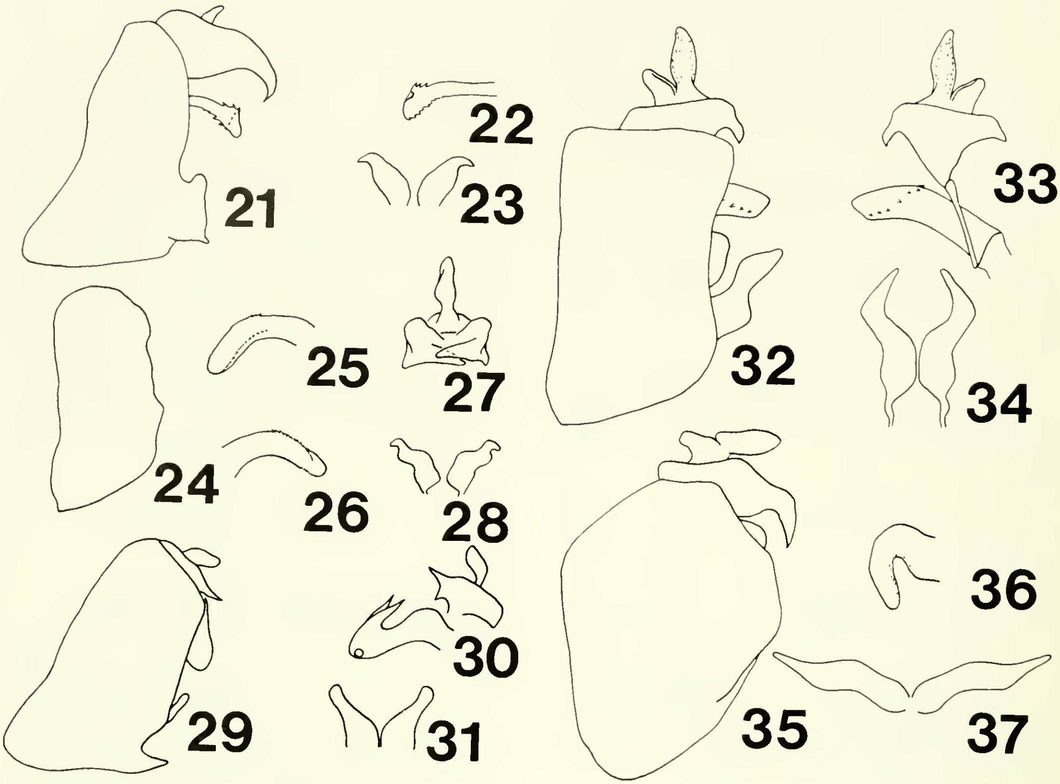
DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: Denmark, Finland, East Germany, West Germany, Poland, Sweden, USSR.

### *Chilodelphax magnifrons* (Crawford), n. comb.
Figs. 21–23

*Megamelus magnifrons* Crawford, 1914:614
*Eurysa magnifrons* (Crawford): Muir and Giffard 1924:8

Beamer (1952a) included four North American species in *Eurysa* but suggested they might belong in *Eurybregma*. Examination of Palearctic *Eurysa* and *Eurybregma* indicates clearly that, based on features of the male genitalia, this species belongs in neither genus. It appears similar to *Chilodelphax silvaticus* Vilbaste as described and illustrated by Kwon (1982); I tentatively place it in *Chilodelphax* Vilbaste (1968).

Distribution records for specimens used in this study are: ALASKA: Ferry, 4 June 1981, S. F. MacLean (9 males, 7 females). Other records are from Beamer (1952a).




Figs. 21–37. Figs. 21–23, *Chilodelphax magnifrons* (Crawford): 21, male genitalia, lateral view, 22, aedeagus, lateral view; 23, styles, caudal view. Figs. 24–28, *Ribautodelphax albostriatus* (Fieber): 24, pygofer, lateral view; 25, 26, aedeagus, lateral view; 27, anal tube, caudal view; 28, styles, caudal view. Figs. 29–31, *Acanthodelphax analis* (Crawford): 29, male genitalia, lateral view; 30, anal tube and aedeagus, lateral view; 31, styles, caudal view. Figs. 32–34, *Kusnezoviella macleani*, n. sp.: 32, male genitalia, lateral view; 33, anal tube and aedeagus, lateral view; 34, styles, caudal view. Figs. 35–37, *Javesella pellucida* (Fabricius): 35, male genitalia, lateral view; 36, aedeagus, lateral view; 37, styles, caudal view.

DISTRIBUTION.—NEARCTIC: Canada: British Columbia; USA: Alaska, Colorado, Montana, Wyoming.

### *Ribautodelphax albostriatus* (Fieber)
Figs. 24–28

*Delphax albostriata* Fieber, 1866:525
*Ribautodelphax albostriatus* (Fieber): Wagner 1963: 170, 176

Distribution records for specimens used in this study are: ALASKA: Inspiration Base Camp (64°N, 148°40′W), 7 June 1981, S. F. MacLean (1 male); Umiat, 8 July 1959, R. Madge (2 males), 20 July 1959 (1 male), J. E. H. Martin, 13 July 1959 (1 male), 16 July 1959 (2 males), 23 July 1959 (2 males). Other records are from Nast (1972). This species was reported from dry grass fields by Ossiannilsson (1978).

DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: Austria, Belgium, Cyprus, Czechoslovakia, Denmark, Finland, France, East Germany, West Germany, Hungary, Italy, Mongolia, Netherlands, Norway, Poland, Portugal, Romania, Spain, Sweden, Switzerland, Tunisia, USSR, Yugoslavia.

### *Acanthodelphax analis* (Crawford), n. comb.
Figs. 29–31

*Megamelus analis* Crawford, 1914: 620
*Delphacodes analis* (Crawford): Muir and Giffard 1924:24

Distribution records for specimens used in this study are: ALASKA: Inspiration Base Camp (64°N, 148°40′W), 7 June 1981, S. F. MacLean (7 males); Hope, Kenai Peninsula, 24 May 1951, W. J. Brown, coll. (3 males, 1 female, 2 nymphs). Other records are from

DuBose (1960) and Wilson and McPherson (1980).

DISTRIBUTION.—NEARCTIC: Canada: Alberta; USA: Alaska, Illinois, Michigan, Minnesota, New York, North Carolina, Wisconsin.

### *Kusnezoviella* Vilbaste

*Kusnezoviella* Vilbaste 1965: 16. Type species *Liburnia dimidiatifrons* Kusnezov, by original designation

The following description is based on a translation from the original Russian supplied by Vilbaste.

Vertex slightly longer than wide, widening anteriorly. Frons with lateral margins almost parallel, converging posteriorly; median carina distinct, forking at juncture with vertex. Antennal scape length subequal to width at apex; pedicel ca 2X length of scape. Beak extending to mesocoxae. Pronotal carinae distinct; lateral carinae curving posterolaterad and disappearing between eye and posterior margin of pronotum. Mesonotal carinae diverging at a 50–60-degree angle. Brachypterous forewings ca 2X longer than wide. Metatibia with 7 teeth (5 + 2) in transverse row at apex on plantar surface; spur foliaceous, with 18 teeth becoming larger apically, apical tooth small.

Pygofer, in lateral view, with caudal margin oblique, slightly concave in middle. Diaphragm with dorsoposteriorly directed extension bearing teeth laterad. Anal tube with pair of elongate, acute spines; bases of spines well separated, distance between them ca 1/2 length of spine. Styles directed posterodorsally, apex acute, base broad. Aedeagus directed caudally, with row of teeth around gonopore, gonopore on dorsal aspect.

### *Kusnezoviella macleani*, n. sp.
Figs. 32–34

Vertex pale beige, one dark brown spot laterally at base on each side, two dark brown spots medially anterior to V-shaped, transverse carina. Frons with carinae pale beige, area between carinae dark brown to pale in middle. Clypeus dark brown with pale, median carina.

Pronota and mesonota pale beige medially, dark brown lateral to lateral carinae. Brachypterous forewing hyaline, light brown. Legs straw-colored with brownish, longitudinal stripes.

Abdomen blackish, marked with pale beige.

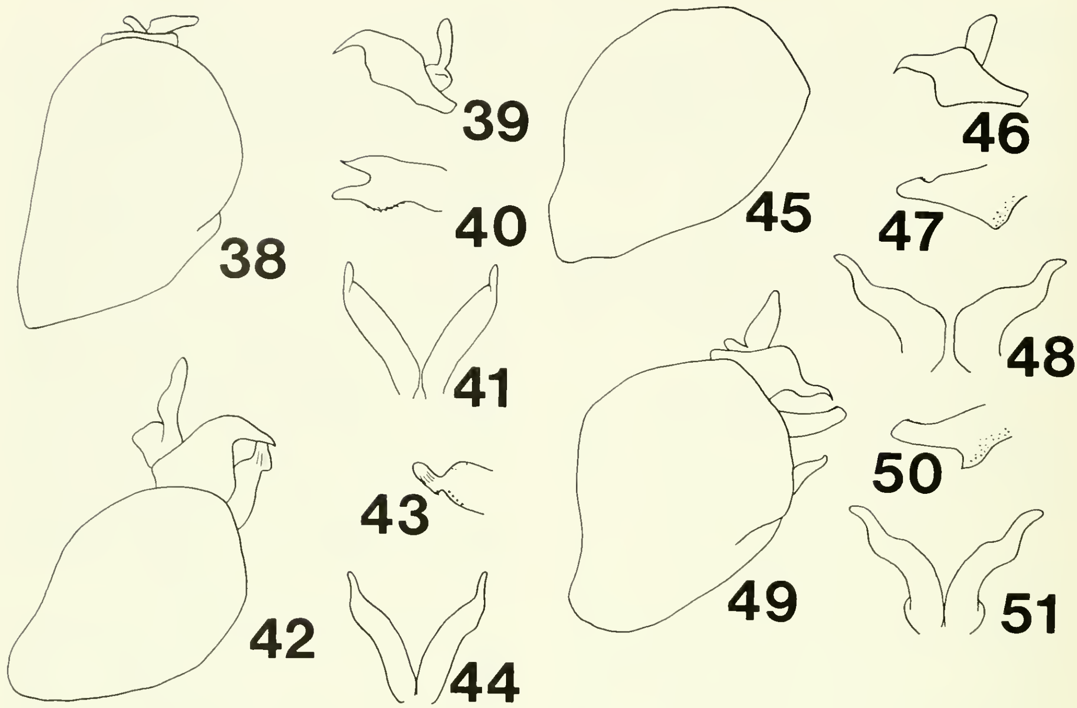
MALE GENITALIA.—Pygofer subcylindrical; in lateral view, height ca 1.5X width; in caudal view, with weak dorsolaterally flaring lobes on lateral margin in dorsal 1/2; ventral margin of diaphragm opening with subtriangular extension, in lateral view, with one small spine on either side, in caudal view. Anal tube subcylindrical, two short, acute spines extending from dorsocaudal margin; each spine separated at base by distance subequal to length of spine. Styles converging at apices, narrowing toward subacute tips; apical 1/2 avicephaliform. Aedeagus subcylindrical, slightly laterally compressed, recurved; gonopore apical; apex appears to be broken but is identical in every specimen; with ca 6–7 teeth extending from near apex on ventral margin anterodorsally and 3 teeth on dorsal margin at point of downward curvature of aedeagus.

TYPES.—HOLOTYPE (male) brachypter with label: "Atkasuk, AKA., mouth of Meade R., 18 June 1977, S. F. MacLean, coll., 770617–03T." ALLOTYPE (female) brachypter, same data; in the Canadian National Collection, Ottawa. PARATYPES: ALASKA: Atkasuq, mouth of Meade R., 17 June 1977, S. F. MacLean, coll. (1 male), 18 June 1977 (1 male); Umiat, 23 July 1959, J. E. H. Martin (3 males); in the University of Kansas collection and collection of S. W. Wilson. These specimens were swept from two species of shrub willow (*Salix alaxensis* [Anderss.] Coville and *S. glauca* L.) (MacLean, personal correspondence); it is possible that their actual host plant may be a grass or sedge found under or near the willows.

### *Javesella pellucida* (Fabricius)
Figs. 35–37

*Fulgora pellucida* Fabricius, 1794:7
*Delphacodes pellucida* (Fabricius): Muir and Giffard 1924:20
*Javesella pellucida* (Fabricius): Fennah 1963:15

Distribution records for specimens used in this study are: ALASKA: Big Delta, 3 July 1951, Mason and McGillis (2 males); Cooper Landing, Kenai Peninsula, 7 June 1951, W. J. Brown (1 male); King Salmon, Naknek R., 3 July 1952, W. R. Mason (1 male), 23 July 1952 (2 males), 1 August 1952 (1 male), 8 August 1952 (1 male); Shaw Creek, M. 289 Rich. Hwy., 11 July 1951, Mason and McGillis




Figs. 38–51. Figs. 38–41, *Javesella obscurella* (Boheman): 38, male genitalia, lateral view; 39, anal tube, lateral view; 40, aedeagus, lateral view; 41, styles, caudal view. Figs. 42–44, *Javesella atrata* (Osborn): 42, male genitalia, lateral view; 43, aedeagus, lateral view; 44, styles, caudal view. Figs. 45–48, *Javesella simillima* (Linnavuori): 45, pygofer, lateral view; 46, anal tube, lateral view; 47, aedeagus, lateral view; 48, styles, caudal view. Figs. 49–51, *Javesella discolor* (Boheman): 49, male genitalia, lateral view; 50, aedeagus, lateral view; 51, styles, caudal view.

(1 male); Umiat, 4 July 1959, R. Madge (2 males), 8 July 1959 (1 male); Unqlakleet, 8 July 1981, R. Madge (1 male). Other records are from Dubose (1960), Muir and Giffard (1924), Nast (1972), and from my collection. *Javesella pellucida* is a vector of viral pathogens of several cereals (Wilson and O'Brien 1987); studies of the biology of this planthopper were summarized by Mochida and Kisimoto (1971).

DISTRIBUTION.—NEARCTIC: Canada: Alberta; USA: Alaska, Connecticut, Illinois, Maine, Massachusetts, New Hampshire, North Carolina, North Dakota, Oregon. PALEARCTIC: Algeria, Austria, Belgium, Czechoslovakia, Denmark, Finland, France, East Germany, West Germany, Great Britain, Hungary, Iceland, Ireland, Italy, Japan, Libya, Mongolia, Morocco, Netherlands, Norway, Poland, Romania, Spain, Sweden, Switzerland, Turkey, USSR, Yugoslavia.

### *Javesella obscurella* (Boheman)
Figs. 38–41

*Delphax obscurella* Boheman, 1847:53
*Javesella obscurella* (Boheman): LeQuesne 1964:57

Distribution records for specimens used in this study are: ALASKA: Atkasuq, 16 June 1977, mouth of Meade R., S. F. MacLean (1 male, 1 female), 17 June 1977 (1 male); 24 July 1977 (2 males); 31 July 1977 (3 males, 2 females); Brooks Range, Happy Valley, 69°05′N, 149°W, 320 m, 6 July 1982, Seppo Keponen, ex. *B. glandulosa* (3 females); Cape Thompson, 23 July 1961, R. Madge (7 males); Umiat, 4 July 1959, R. Madge (1 male), 8 July 1959 (1 male); USSR: Chaun Bay, 14 August 1977, S. F. MacLean, Jr., ex. *Poa* and *Festuca* (1 male, 3 parasitized males, 3 females, 6 nymphs). Other records are from Nast (1972). Records from New York given in Metcalf (1943) come from before the widespread use of genitalic features in delphacid identification and, thus,

are probably in error. This species is a vector of viral pathogens of cereals (Wilson and O'Brien 1987); the biology of it on cereal crops was summarized by Ossiannilsson (1978).

DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: Austria, Belgium, Bulgaria, Czechoslovakia, Denmark, Finland, France, East Germany, West Germany, Great Britain, Hungary, Ireland, Italy, Mongolia, Netherlands, Norway, Poland, Portugal, Romania, Sweden, Switzerland, Turkey, USSR, Yugoslavia.

### *Javesella atrata* (Osborn), n. comb.

Figs. 42–44

*Delphacodes atrata* Osborn, 1938:344

Specimens from Alaska were not available for this study; illustrations were made from a "paramorphotype" with the following collecting data: OHIO: Rome, 19 July 1946, R. H. Beamer. Beamer (1951) recorded this species from Ketchikan, Alaska, as well as the other localities given below.

DISTRIBUTION.—NEARCTIC: USA: Alaska, Connecticut, Illinois, New Hampshire, New York, Ohio.

### *Javesella simillima* (Linnavuori)

Figs. 45–48

*Calligypona simillima* Linnavuori, 1948:45
*Delphacodes saileri* Beamer 1952b:114. *New synonymy*
*Javesella simillima* (Linnavuori): Nast 1972:68

I was unable to determine who first placed this species in *Javesella*. Based on information given by Hulden (1974), it appears to be Linnavuori (1969), a paper which was unavailable to me. In the foregoing synonymy I list Nast (1972) as my reference for first placement in *Javesella*.

Distribution record for the specimen used in this study is: ALASKA: Umiat, 4 July 1959, R. Madge (1 male). Other records are from Beamer (1952b) and Nast (1972). This species is reported from *Eriophorum* and *Carex* by Ossiannilsson (1978).

DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: Finland, USSR.

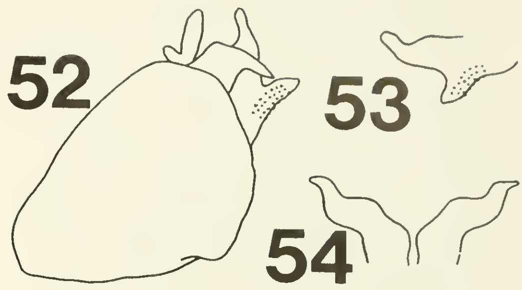
### *Javesella discolor* (Boheman)

Figs. 49–51

*Delphax discolor* Boheman, 1847:61
*Javesella discolor* (Boheman): LeQuesne 1964:57

Distribution records for specimens used in this study are: ALASKA: Umiat, 3 July 1959, J. E. H. Martin (1 male); 4 July 1959, R. Madge (4 males), 8 July 1959 (3 males). Other records are from Nast (1972). This species has been reported to be a vector of viral pathogens of cereals (Wilson and O'Brien 1987); host plants were summarized by Ossiannilsson (1978).

DISTRIBUTION.—NEARCTIC: USA: Alaska. PALEARCTIC: Algeria, Austria, Belgium, Czechoslovakia, Denmark, Finland, France, East Germany, West Germany, Great Britain, Ireland, Italy, Mongolia, Netherlands, Norway, Poland, Romania, Sweden, Switzerland, USSR.




Figs. 52–54. *Javesella arcanastyla* (Beamer): 52, male genitalia, lateral view; 53, aedeagus, lateral view; 54, styles, caudal view.

### *Javesella arcanastyla* (Beamer), n. comb.

Figs. 52–54

*Delphacodes arcanastyla* Beamer, 1948:101

Distribution record for the specimen used in this study is: ALASKA: Matanuska, 9 June 1944, J. C. Chamberlain, Rotary Traps, 46–7695. Other records are from Beamer (1948) and the Michigan State University collection.

DISTRIBUTION.—NEARCTIC: USA: Alaska, Michigan, Washington, Wisconsin, Wyoming.

## COMMENTS ON DISTRIBUTION

Localities represented in the material used for this study range from the Kenai and Alaska peninsulas in the south through east central Alaska extending to ca 100 km from the northern coast. Three other localities represent coastal sites, one on the north coast in the western one-third of the state, one on the west coast above the Arctic circle, and one on the

central west coast. Only one record is from the southeastern portion of the state.

One of the 15 delphacid species is recorded only from Alaska (*K. macleani*); 3 species are Holarctic in distribution (*A. subarctica*, *J. pellucida*, and *M. flavus*), 4 are Nearctic (*A. analis*, *C. magnifrons*, *J. arcanastyla*, and *J. atrata*), and 7 are Palearctic (*C. wilhelmi*, *J. discolor*, *J. obscurella*, *J. simillima*, *N. eburneocarinatus*, *R. albostriatus*, and *U. excisa*). One of the seven Palearctic planthoppers (*N. eburneocarinatus*) appears to have an amphi-Beringean distribution; five of the seven have only been collected north of the Brooks Range; all seven are apparently restricted to tundra habitats in Alaska. The diversity of the Alaskan delphacid fauna is comparable to that reported by Vilbaste (1980), who listed 10 species from the Kamchatka Peninsula.

## Acknowledgments

Thanks are tendered to Dr. G. G. E. Scudder, Department of Entomology, University of British Columbia, Vancouver, Canada, who recommended me as someone who might be able to identify Alaskan delphacids; Dr. S. F. MacLean, Jr., Department of Zoology, University of Alaska, Fairbanks, for providing detailed information on the collecting localities; Dr. K. G. A. Hamilton, Biosystematics Research Centre, Agriculture Canada, Ottawa, for the loan of material; the late Dr. J. Vilbaste, Institute of Zoology and Botany, Academy of Sciences, Tartu, Estonian SSR, who suggested the generic placement of the new species and provided an English translation of his description; Drs. M. Asche, H. Hoch, and R. Remane, Fachbereich Biologie-Zoologie, Philipps Universität, Marburg, West Germany, for their invaluable aid in identifying Palearctic material; and Dr. L. B. O'Brien for commenting on the manuscript. I appreciate support for work at Philipps Universität, where some of this research was done, from the German Academic Exchange and the Graduate School, Central Missouri State University.

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## TAXA IN THE HOMOPTERA, AUCHENORRHYNCHA DESCRIBED BY PAUL W. OMAN

### Homoptera

Fossil Cicadelloidea
- *Mesojassoides* Oman 1937. Colorado.
- *Mesojassoides gigantea* Oman 1937. Colorado.

**Fulgoridae**
- *Poblicia texana* Oman 1936. Texas.

**Cicadellidae**

Subfamily
- Dorycephalinae
- Neocoelidiinae
- Nioniinae
- Xerophloeinae

Tribe
- Acinopterini
- Cochlorinini
- Dorycephalini
- Mesamiinae
- Neocoelidiini
- Nionini
- Scaphoideini
- Scaphytopiini
- Xerophloeini

Genera and Subgenera
- *Aceratagallia* (*Bergallia*) Oman 1938. Argentina.
- *Aflexia* Oman 1949. Illinois.
- *Agalliana* Oman 1933. Brazil.
- *Agalliopsis* (*Agallaria*) Oman 1949. Indiana.
- *Agalliota* Oman 1938. Mexico.
- *Agelina* Oman 1938. Argentina.
- *Agudus* Oman 1938. Argentina.
- *Alaca* Oman 1938. Argentina.
- *Allygiella* Oman 1949. California.
- *Ankosus* Oman & Musgrave 1975. Oregon.
- *Aplanus* Oman 1949. Colorado.
- *Arrugada* Oman 1938. Bolivia.
- *Atanus* Oman 1938. Bolivia.
- *Auridius* Oman 1949. Colorado.
- *Bahita* Oman 1938. Brazil.
- *Baldulus* Oman 1934. Arizona.
- *Baroma* Oman 1938. Argentina.
- *Bathysmatophorus* (*Hylaius*) Oman & Musgrave 1975. Oregon.
- *Benala* Oman 1938. Bolivia.
- *Bolarga* Oman 1938. Bolivia.
- *Bonamus* Oman 1938. Argentina.
- *Bonneyana* Oman 1949. Utah.
- *Brasa* Oman 1938. Hispaniola.
- *Brazosa* Oman 1939. Brazil.
- *Brenda* Oman 1941. California.
- *Brincadorus* Oman 1938. Brazil.
- *Bythonia* Oman 1938. Bolivia.
- *Cabrulus* Oman 1949. Colorado.
- *Caladonus* Oman 1949. California.
- *Cantura* Oman 1949. Eastern USA and Canada.
- *Caphodus* Oman 1938. Argentina.
- *Cariancha* Oman 1938. Brazil.
- *Cazenus* Oman 1949. New Mexico.
- *Cerrillus* Oman 1938. Brazil.
- *Cetexa* Oman 1949. Colorado.
- *Coelidiana* Oman 1938. Brazil.
- *Colimona* Oman 1949. Arizona.
- *Conala* Oman 1938. Brazil.
- *Cortona* Oman 1938. Argentina.
- *Cribrus* Oman 1949. Minnesota.
- *Crumbana* Oman 1949. Tennessee.
- *Cumora* Oman 1938. Argentina.
- *Daltonia* Oman 1949. Texas.
- *Danbara* Oman 1949. Washington, D. C.
- *Decua* Oman 1949. Arizona.
- *Deltanus* Oman 1949. Texas.
- *Deltella* Oman 1949. Florida.
- *Deltocephalus* (*Haldorus*) Oman 1938. Bolivia.
- *Destria* Oman 1949. Florida.
- *Dikrella* Oman 1949. New Mexico.
- *Dorycephalus* (*Attenuipyga*) Oman 1949. Florida.
- *Egenus* Oman 1939. Argentina.
- *Endria* Oman 1949. Virginia.
- *Errhomus* Oman 1938. Washington.
- *Errhomus* (*Carsonus*) Oman 1938. Colorado.
- *Eulonus* Oman 1949. California.
- *Euragallia* Oman 1938. Brazil.
- *Eusama* Oman 1949. Arizona.
- *Eusora* Oman 1949. Colorado.
- *Extrusanus* Oman 1949. New York.
- *Faltala* Oman 1938. Argentina.
- *Fitchana* Oman 1949. New York.
- *Floridonus* Oman 1949. Florida.
- *Fridonus* Oman 1949. Texas.
- *Frigartus* Oman 1949. Colorado.
- *Friscanus* Oman 1939. California.
- *Garapita* Oman 1938. Argentina.
- *Giprus* Oman 1949. California.
- *Hebexa* Oman 1949. Utah.
- *Hecullus* Oman 1949. Colorado.
- *Hegira* Oman 1938. Argentina.

*Hordnia* Oman 1949. California.
*Kanorba* Oman 1938. Brazil.
*Keonolla* Oman 1949. Washington.
*Kunzeana* Oman 1949. Arizona.
*Lemellus* Oman 1949. Colorado.
*Limbanus* Oman 1949. California.
*Lycioides* Oman 1949. Arizona.
*Manzutus* Oman 1949. Arizona.
*Marathonia* Oman 1949. Texas.
*Mexara* Oman 1949. Arizona.
*Negosiana* Oman 1949. Southeastern U.S.
*Neobala* Oman 1938. Bolivia.
*Neonirvana* Oman 1936. Coasta Rica.
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*Nigridonus* Oman 1949. Arizona.
*Nurenus* Oman 1949. Arizona.
*Onura* Oman 1938. Argentina.
*Orocastus* Oman 1949. Montana.
*Pasarenus* Oman 1949. Colorado.
*Pazu* Oman 1949. Arizona.
*Peconus* Oman 1949. Arizona.
*Phlepsanus* Oman 1949. Arizona.
*Quontus* Oman 1949. Colorado.
*Rosenus* Oman 1949. Iowa.
*Sobara* Oman 1949. Texas.
*Telusus* Oman 1949. Colorado.
*Texananus* (*Excultanus*) Oman 1949. Florida.
*Thatuna* Oman 1938. Idaho.
*Tiaja* Oman 1941. California.
*Verdanus* Oman 1949. Alaska.
*Zabrosa* Oman 1949. Brazil.

Species and Subspecies

*Aceratagallia abrupta* Oman 1933. Arizona.
*Aceratagallia accola* Oman 1933. USA.
*Aceratagallia* (*Bergallia*) *attenuata* Oman 1938. Argentina.
*Aceratagallia aplopappi* Oman 1933. USA.
*Aceratagallia arida* Oman 1933. USA.
*Aceratagallia calcaris* Oman 1933. USA.
*Aceratagallia catalina* Oman 1938. Brazil.
*Aceratagallia chileana* Oman 1938. Chile.
*Aceratagallia cinerea* Oman 1933. USA.
*Aceratagallia compacta* Oman 1933. California.
*Aceratagallia confusa* Oman 1938. Argentina.
*Aceratagallia curta* Oman 1933. Arizona.
*Aceratagallia curvata* Oman 1933. USA.
*Aceratagallia dondia* Oman 1933. USA.
*Aceratagallia fuscoscripta* Oman 1933. USA.
*Aceratagallia grisea* Oman 1935. Arizona.
*Aceratagallia helveola* Oman 1933. USA.
*Aceratagallia humilis* Oman 1933. USA.
*Aceratagallia lateralis* Oman 1938. Argentina.
*Aceratagallia lobata* Oman 1933. USA.
*Aceratagallia nana* Oman 1933. Arizona.
*Aceratagallia nanella* Oman 1933. Arizona.
*Aceratagallia neosignata* Oman 1938. Argentina.
*Aceratagallia nitidula* Oman 1933. Arizona.
*Aceratagallia obscura* Oman 1933. USA.
*Aceratagallia ovata* Oman 1935. Arizona.
*Aceratagallia pallida* Oman 1933. Utah, Arizona.
*Aceratagallia poudris* Oman 1933. Colorado.
*Aceratagallia robusta* Oman 1933. USA.
*Aceratagallia sordida* Oman 1933. Honduras, Mexico, Texas.
*Aceratagallia texana* Oman 1933. Texas.
*Aceratagallia truncata* Oman 1935. California.
*Aceratagallia unica* Oman 1938. Argentina.
*Aceratagallia vastitatis* Oman 1933. USA.
*Aceratagallia vulgaris* Oman 1933. Kansas.
*Agallia abnormis* Oman 1938. Argentina.
*Agallia acuticauda* Oman 1933. Haiti.
*Agallia atromaculata* Oman 1938. Bolivia.
*Agallia basalis* Oman 1938. Bolivia.
*Agallia basifusca* Oman 1938. Bolivia.
*Agallia bifurcata* Oman 1938. Bolivia.
*Agallia bicolor*. Oman 1933. West Indies.
*Agallia bidigitata* Oman 1933. Guatemala.
*Agallia blanda* Oman 1938. Argentina.
*Agallia brevicaudata* Oman 1938. Brazil.
*Agallia caudata* Oman 1938. Bolivia.
*Agallia clara* Oman 1938. Brazil.
*Agallia configurata* Oman 1933. Puerto Rico.
*Agallia constricta* cubana Oman 1933. Cuba
*Agallia corumba* Oman 1938. Brazil.
*Agallia depleta* Oman 1938. South America.
*Agallia didactylata* Oman 1933. Arizona.
*Agallia dorsata* Oman 1938. Argentina.
*Agallia extensa* Oman 1938. Bolivia.
*Agallia fumida* Oman 1938. Colombia.
*Agallia hyalina* Oman. 1938. Brazil.
*Agallia hystricula* Oman 1933. Costa Rica.
*Agallia incerta* Oman 1938. Argentina.
*Agallia incisa* Oman 1938. Brazil.
*Agallia incongrua* Oman 1938. Argentina.
*Agallia ingens* Oman 1933. Central America.
*Agallia inornata* Oman 1938. Brazil.
*Agallia manaosa* Oman 1938. Brazil.
*Agallia minuenda* Oman 1938. Brazil.
*Agallia munda* Oman 1933. West Indies.
*Agallia neoalbidula* Oman 1938. Brazil.
*Agallia nigerrima* Oman 1938. Brazil.
*Agallia obesa* Oman 1933. USA.
*Agallia pumila* Oman 1971. USA.
*Agallia peneconstricta* Oman 1933. Honduras.
*Agallia quadrata* Oman 1938. Brazil, Bolivia.
*Agallia quadripunctata excavata* Oman 1933. USA.
*Agalliana ancora* Oman 1934. Bolivia.
*Agalliana ensigera* Oman 1934. South America.

*Agalliana fusca* Oman 1934. South America.
*Agalliana grossa* Oman 1934. Argentina.
*Agalliana mediana* Oman 1938. Argentina.
*Agalliana puella* Oman 1938. Colombia.
*Agalliopsis abietaria* Oman 1970. USA.
*Agalliopsis acuminata* Oman 1934. Mexico.
*Agalliopsis agrestis* Oman 1934. Mexico.
*Agalliopsis ancistra* Oman 1970. USA.
*Agalliopsis ancoralis* Oman 1933. Mexico.
*Agalliopsis atra* Oman 1934. Arizona, Mexico.
*Agalliopsis brunnea* Oman 1933. Mexico, Honduras.
*Agalliopsis cervina* Oman 1933. Kansas.
*Agalliopsis cincta* Oman 1933. Florida.
*Agalliopsis conformis* Oman 1933. Dominican Republic.
*Agalliopsis disparillis* Oman 1938. Colombia.
*Agalliopsis distincta* Oman 1934. Mexico.
*Agalliopsis dubiosa* Oman 1933. Arizona.
*Agalliopsis elegans* Oman 1938. Brazil.
*Agalliopsis exilis* Oman 1933. Colorado.
*Agalliopsis florida* Oman 1935. Florida.
*Agalliopsis fuscosignata* Oman 1933. Arizona.
*Agalliopsis fuscosignata minor* Oman 1933. Arizona.
*Agalliopsis gracilis* Oman 1934. Mexico.
*Agalliopsis hamatilis* Oman 1970. Mexico.
*Agalliopsis huachucae* Oman 1933. Arizona.
*Agalliopsis inscripta* Oman 1934. Guatemala.
*Agalliopsis longipennis* Oman 1934. Mexico.
*Agalliopsis magnifica* Oman 1933. Mexico.
*Agalliopsis majesta* Oman 1934. Mexico.
*Agalliopsis neopepino* Oman 1935. Cuba.
*Agalliopsis nervata* Oman 1934. Mexico.
*Agalliopsis novella emulata* Oman 1938. Argentina.
*Agalliopsis novella vicosa* Oman 1938. Brazil.
*Agalliopsis novellina* Oman 1935. USA.
*Agalliopsis oculata* Oman 1933. California.
*Agalliopsis ornata* Oman 1938. Brazil.
*Agalliopsis ornaticollis* Oman 1938. Argentina.
*Agalliopsis peneoculata* Oman 1933. USA.
*Agalliopsis peruviana* Oman 1938. Peru.
*Agalliopsis pulchella* Oman 1938. Argentina.
*Agalliopsis punctata* Oman 1934. Mexico.
*Agalliopsis reflexa* Oman 1970. Venezuela.
*Agalliopsis similis* Oman 1934. Mexico.
*Agalliopsis sonorensis* Oman 1970. Mexico.
*Agalliopsis stella* Oman 1970. USA.
*Agalliopsis teapae* Oman 1934. Mexico.
*Agalliopsis tincta* Oman 1938. Brazil.
*Agalliopsis variabilis* Oman 1933. USA.
*Agalliopsis vonella* Oman 1938. Colombia.
*Agalliota clavata* Oman 1938. Brazil.
*Agalliota dentata* Oman 1938. Brazil.
*Agalliota parallela* Oman 1938. Brazil.
*Agalliota parma* Oman 1938. Brazil.
*Agalliota scutaria* Oman 1938. Argentina.
*Agelina punctata* Oman 1938. South America.
*Agudus typicus* Oman 1938. South America
*Alaca longicauda* Oman 1938. Argentina.
*Attenuipyga balli* Oman 1985. USA.
*Baldulus montanus* Oman 1934. Arizona.
*Baroma reticulata* Oman 1938. Argentina.
*Bonamus lineatus* Oman 1938. Argentina.
*Brincadorus laticeps* Oman 1938. South America.
*Caphodus maculatus* Oman 1938. Brazil.
*Cariancha cariboba* Oman 1938. Brazil.
*Ceratagallia arroya* Oman 1939. California.
*Ceratagallia artemisia* Oman 1939. Idaho, Utah.
*Ceratagallia califa* Oman 1939. California.
*Ceratagallia canona* Oman 1939. California.
*Ceratagallia delta* Oman 1939. California.
*Ceratagallia loca* Oman 1939. California.
*Ceratagallia loma* Oman 1939. California.
*Ceratagallia longipes* Oman 1939. California.
*Ceratagallia ludora* Oman 1939. California.
*Ceratagallia lupina* Oman 1939. California.
*Ceratagallia neodona* Oman 1939. Nevada.
*Ceratagallia neovata* Oman 1939. California.
*Ceratagallia pera* Oman 1939. California.
*Ceratagallia pudica* Oman 1939. Arizona.
*Ceratagallia socala* Oman 1939. California.
*Ceratagallia tristis* Oman 1939. California.
*Cortona minuta* Oman 1938. Argentina.
*Cuerna alba* Oman & Beamer 1944. New Mexico.
*Cuerna alta* Oman & Beamer 1944. New Mexico.
*Cuerna arida* Oman & Beamer 1944. Arizona.
*Cuerna balli* Oman & Beamer 1944. Arizona.
*Cuerna curvata* Oman & Beamer 1944. California.
*Cuerna dixiana* Oman & Beamer 1944. Utah, Nevada.
*Cuerna gladiola* Oman & Beamer 1944. California.
*Cuerna mexicana* Oman & Beamer 1944. Mexico.
*Cuerna obesa* Oman & Beamer 1944. New Mexico, Texas.

*Cuerna obtusa* Oman & Beamer 1944. Arizona.
*Cuerna occidentalis* Oman & Beamer 1944. California.
*Cuerna yuccae* Oman & Beamer 1944. California, Utah, Arizona.
*Cumora angulata* Oman 1938. Argentina.
*Deltocephalus grex* Oman 1940. Arizona.
*Deltocephalus dorsti* Oman 1940. Utah.
*Deltocephalus laredanus* Oman 1934. Texas.
*Deltocephalus lineatifrons* Oman 1931. Colorado.
*Deltocephalus playensis* Oman 1940. Arizona.
*Dikraneura cedrelae* Oman 1937. Puerto Rico.
*Dikraneura lentrosemae* Oman 1937. Puerto Rico.
*Dorycara platyrhyncha setosa* Oman 1985. USA.
*Egenus acuminatus* Oman 1938. Argentina.
*Empoasca curveola* Oman 1936. Argentina.
*Empoasca dolonis* Oman 1936. Argentina.
*Empoasca ensiformis* Oman 1938. Oregon.
*Empoasca fuscoviridis* Oman 1938. Colorado.
*Empoasca indenta* Oman 1938. Utah.
*Empoasca insularis* Oman 1936. Puerto Rico.
*Empoasca longispina* Oman 1936. Argentina.
*Empoasca missiona* Oman 1936. Argentina.
*Empoasca neaspersa* Oman 1938. Western USA.
*Empoasca ornata* Oman 1936. Bolivia.
*Empoasca papayae* Oman 1937. Puerto Rico.
*Empoasca peregrina* Oman 1936. Peru.
*Empoasca perelegans* Oman 1936. Neotropical.
*Empoasca phaseola* Oman 1936. Costa Rica.
*Empoasca rubraza* Oman 1936. South America.
*Empoasca setigera* Oman 1936. Argentina.
*Empoasca trifurcata* Oman 1936. Argentina.
*Empoasca vastitatis* Oman 1938. New Mexico.
*Empoasca vermispina* Oman 1938. California.
*Empoasca xerophila* Oman 1938. Colorado.
*Euragallia albopunctata* Oman 1938. Brazil.
*Euragallia attenuata* Oman 1938. Brazil.
*Euragallia lata* Oman 1938. Brazil.
*Euragallia magnicauda* Oman 1938. Brazil.
*Euragallia major breviata* Oman 1938. Brazil.
*Errhomus (Carsonus) aridus furcatus* Oman 1938. Washington.
*Errhomus (Carsonus) aridus incertus* Oman 1938. California.
*Errhomus brevis brevis* Oman 1987. Washington.
*Errhomus brevis klickitat* Oman 1987. Washington.
*Errhomus filamentus* Oman 1952. Oregon.
*Errhomus idahoensis* Oman 1987. Idaho.
*Errhomus (Carsonus) irroratus spicatus* Oman 1938. Oregon.
*Errhomus josephi* Oman 1987. Oregon, Washington.
*Errhomus lineatus umatilla* Oman 1987. Oregon.
*Errhomus medialis medialis* Oman 1987. Oregon.
*Errhomus medialis minutus* Oman 1987. Oregon.
*Errhomus medialis truncus* Oman 1987. Oregon.
*Errhomus ochoco.* Oman 1987. Oregon.
*Errhomus paradoxus* Oman 1987. Washington.
*Errhomus reflexus* Oman 1987. Washington.
*Errhomus satus* Oman 1987. Washington.
*Errhomus serratus serratus* Oman 1987. Oregon.
*Errhomus serratus instabilis* Oman 1987. Washington.
*Errhomus serratus affinis* Oman 1987. Idaho.
*Errhomus simcoe simcoe* Oman 1987. Washington.
*Errhomus simcoe minor* Oman 1987. Washington.
*Errhomus similis* Oman 1952. Washington.
*Errhomus similis socius* Oman 1987. Washington.
*Errhomus similis relativus* Oman 1987. Washington.
*Errhomus sobrinus sobrinus* Oman 1987. Washington.
*Errhomus sobrinus confinis* Oman 1987. Washington.
*Errhomus sobrinus dubiosus* Oman 1987. Washington.
*Errhomus sobrinus nanus* Oman 1987. Oregon.
*Errhomus sobrinus kahlotus* Oman 1987. Oregon.
*Errhomus solus* Oman 1987. Montana.
*Errhomus variabilis variabilis* Oman 1987. Washington, Idaho.
*Errhomus variabilis pallidus* Oman 1987. Oregon.
*Errhomus variabilis calvus* Oman 1987. Washington, British Columbia.
*Errhomus winquatt* Oman 1987. Oregon.
*Errhomus wolfei* Oman 1952. Washington.
*Errhomus zonarius* Oman 1987. Washington.

*Faltata brachyptera* Oman 1938. Argentina.
*Fridonus concanus* Oman. 1949. Texas.
*Garapita garbosa* Oman 1938. Argentina.
*Hebecephalus scriptanus* Oman 1934. Arizona.
*Hebexa incognita* Oman 1949. Utah, Washington.
*Hegira brunnea* Oman 1938. Argentina.
*Helochara delta* Oman 1943. California.
*Joruma neascripta* Oman 1937. Puerto Rico.
*Kanorba reflexa* Oman 1938. Brazil.
*Koebelia inyoensis* Oman 1972. California.
*Krisna insularis* Oman 1936. Puerto Rico.
*Laevicephalus angelus* Oman 1937. California.
*Laevicephalus aridus* Oman 1934. Arizona.
*Laevicephalus bocanus* Oman 1934. Texas.
*Laevicephalus cartwrighti* Oman 1932. California.
*Laevicephalus excavatus* Oman 1931. California, Oregon.
*Laevicephalus incongruus* Oman 1937. California.
*Laevicephalus joaquinus* Oman 1937. California.
*Laevicephalus pacificus 1937. California.*
*Laevicephalus siskiyou* Oman 1937. USA.
*Laevicephalus uhleri* Oman 1931. USA.
*Laevicephalus wilsoni* Oman 1932. California.
*Lystridea nuda* Oman 1938. California.
*Neocoelidia beameri* Oman 1931. Texas.
*Neocoelidia distincta* Oman 1931. Arizona, Texas.
*Neocoelidia fuscovittata* Oman 1931. Arizona.
*Neocoelidia penelineata* Oman 1931. California, Nevada.
*Neocoelidia texana* Oman 1931. Texas.
*Neonirvana hyalina* Oman 1936. Costa Rica.
*Onura eburneola* Oman 1938. Argentina.
*Pagaronia confusa* Oman 1938. California.
*Pagaronia furcata* Oman 1938. California.
*Paracoelidia fusconeura* Oman 1930. Arizona.
*Phlepsius divergens* Oman 1931. Texas.
*Phlepsius obvius* Oman 1931. Texas.
*Protalebra brunnea* Oman 1937. Puerto Rico.
*Sanctanus tectus* Oman 1934. Virginia, South Carolina
*Scaphoidula dentata* Oman 1937. St. Lucia.
*Scaphoidula incisa* Oman 1937. Central America.
*Scaphoidula unica* Oman 1937. Brazil.
*Tiaja arenaria* Oman 1972. California.
*Tiaja cruzensis* Gill & Oman 1982. California.
*Tiaja montara* Oman 1941. California.
*Tiaja ventura* Oman 1941. California.
*Thatuna gilletti* Oman 1938. Idaho.
*Xerophloea carinata* Oman 1936. Argentina.
*Xerophloea carinata gigas* Oman 1936. Argentina.
*Xerophloea cephalica* Oman 1936. Argentina.
*Xerophloea difformis* Oman 1936. Argentina.
*Xerophloea elegans* Oman 1936. Argentina.
*Xerophloea elongata* Oman 1936. Argentina.
*Xerophloea magna* Oman 1936. Argentina.

# INDEX

New names are indicated by **boldface** type, invalid names by *italics*.